

GENERAL ZOOLOGY

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1947

FOURTH EDITION

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PREFACE

To the Fourth Edition

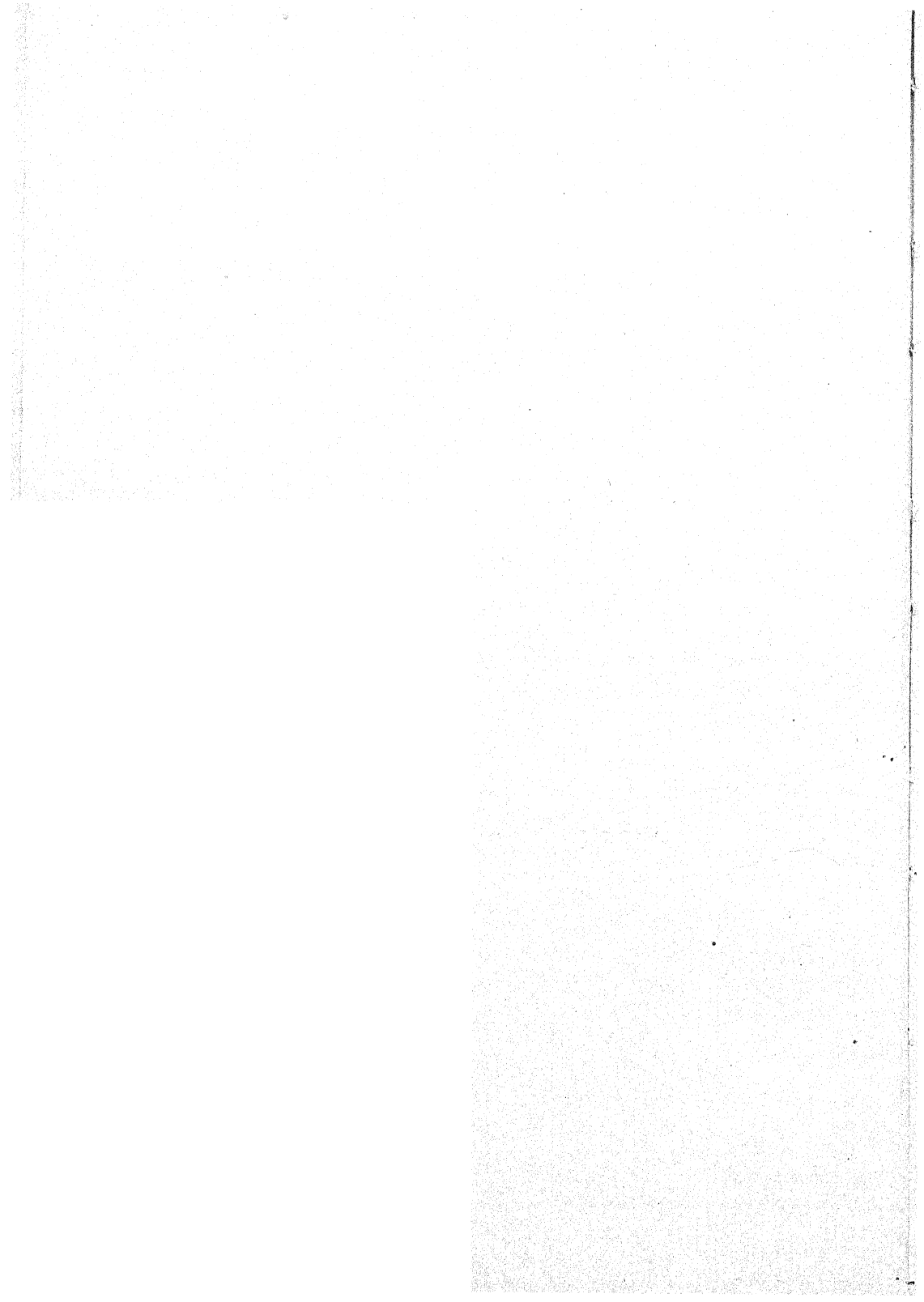
This edition represents a careful editing and revision of text and illustrations. A chapter on the organ systems of invertebrates has been added to serve as a review of the chapters on invertebrates and to facilitate comparisons with the accounts of organ systems in vertebrates. This brings the book up to date and, we hope, will make it as useful in the current educational turmoil as it seems to have been throughout the past twenty years.

The chapters dealing with the general aspects of zoölogical science have been recast as necessary; the chapters on the animal kingdom have been reworked and in places extended. The book continues the plan of earlier editions in its treatment of principles as well as phyla. We believe that this combination still finds favor in the great majority of American institutions, as well as in our own. As in each previous revision, much time has been spent upon the improvement of old figures and the preparation of new ones.

We wish to renew our acknowledgments to those contributing to the earlier editions. The acknowledgments of figures appear in the legends.

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UNIVERSITY OF MISSOURI
Columbia, Missouri
April 1, 1947



PREFACE

To the Third Edition

This edition follows the lines of the preceding one, except for a new mode of introduction. In correlation with this change, Chapter 2 of the 1933 edition has been eliminated and a chapter upon the Chordata has been added to complete the survey of animal types. The other chapters have been fully edited, and some have been substantially modified. Chapters 1 to 6 thus cover the more important general aspects of zoölogical science, except ecology and evolution. Principles of ecology, like the history of zoölogy, are presented as opportunity offers throughout the work. Evolution is again reserved for the final chapter. This reorganization makes it easier to use the volume in a course beginning with unicellular forms and ending with the topics included in the earlier chapters. As with earlier editions the illustrations have received special attention and important additions have been made, notably the original figures in Chapter 7. The junior author is primarily responsible for Chapters 1 to 6, inclusive, and has read critically the remainder of the volume.

While the chapters reviewing the animal phyla have received full consideration, greater attention has been given to the revision of the chapters dealing with subject matter more closely related to twentieth-century developments in zoölogy. Although a survey of the animal kingdom has its place in an elementary course, the authors have the conviction that eventually the field will belong to textbooks that feature the important general aspects of zoölogical science, as we have attempted to do in this volume, and not to those that merely plod through the animal kingdom from amoeba to man, adding a little relief here and there in the form of brief comments upon modern zoölogical subject matter.

We wish to renew our previous acknowledgments to those contributing to the earlier editions and so to this one. Valuable assistance has been rendered in the current revision by Miss Helen Hunt and Mr. Charles Schwartz, as artists, and Miss Orla Selby, as typist,

whom we have employed at our personal expense as their other duties permitted. The acknowledgments of figures and statements of permission to use the same appear in the legends.

W. C. CURTIS
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UNIVERSITY OF MISSOURI
Columbia, Missouri
June 1, 1938

PREFACE

To the Second Edition

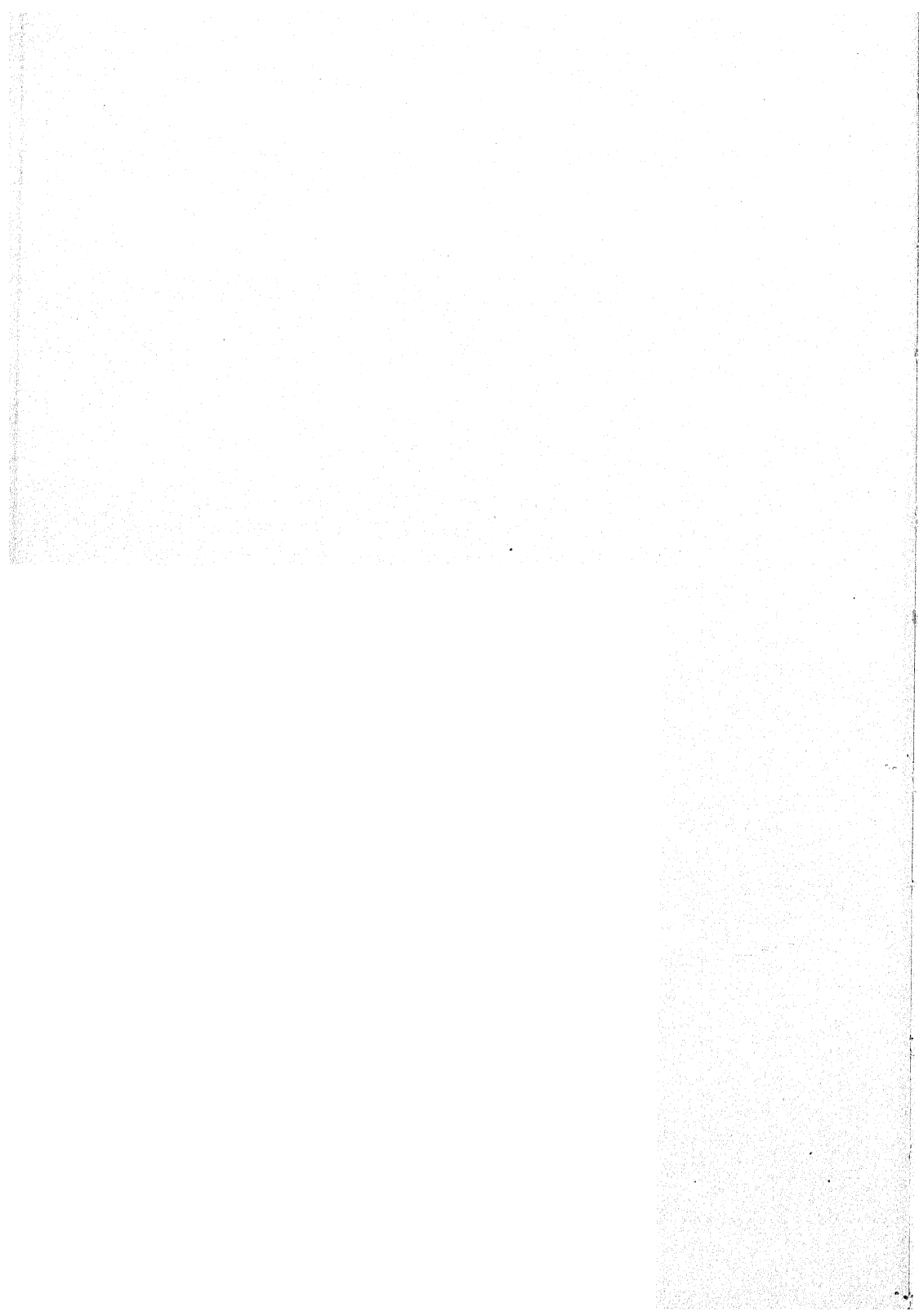
The present edition represents a complete reorganization as well as rewriting of many portions of the text. Reduction of certain parts has made possible the addition of chapters upon phyla not included in the first edition and thus a more comprehensive survey of the Animal Kingdom, without undue restriction of the chapters dealing with general zoölogical problems. These revisions have produced what is virtually a new book which we think will prove better and more usable than the first edition.

The junior author is primarily responsible for Chapters 3-7, inclusive, and has critically edited the remainder of the book. Doctor Jeffers has assisted both of the authors in every phase of the revision.

We wish to acknowledge the assistance of our colleagues Professors Rudolf Bennitt and F. H. Woods, who have read certain chapters and made suggestions as a result of their experience with the previous edition in classes. Many valued suggestions have been received from individuals in other institutions where the first edition has been used. Miss Coral Fleenor, biological artist of the University of Missouri, has assisted with illustrations. The acknowledgments of figures and statements of permission to use the same appear in the legends.

W. C. CURTIS
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UNIVERSITY OF MISSOURI
Columbia, Missouri
March 1, 1933



PREFACE

To the First Edition

Although prefaces are commonly forgotten, if indeed they are read by teachers, it seems that one must say something regarding the origin and nature of a new textbook, particularly in a field that is already well occupied. The present volume is the outcome of a work projected some years ago by the senior author as a formal organization of the course in General Zoölogy that has been developed at the University of Missouri during the past twenty-five years. Historically, it is the descendant of the course in General Biology that was introduced at the Johns Hopkins University by Huxley's student, Newell Martin, and later developed in that institution by E. A. Andrews. From Johns Hopkins and also from its original source in Huxley and later teachers in England, like T. J. and W. N. Parker, this early attempt to teach the principles of biological science has influenced instruction in many American institutions.

At the University of Missouri the course began as General Biology but was restricted to the field of Zoölogy with the establishment of a separate department of Botany. The essential feature of this instruction in General Zoölogy is that a limited number of animals are selected to illustrate certain biological principles and only incidentally as representatives of particular phyla. This is in contrast with what may be called the "phylum" scheme of instruction, which has been widely prevalent during the past twenty years and is represented by well-known textbooks. The latter form of instruction seems to have originated in the old-time courses in Natural History, represented by books like Tenney's "Manual of Zoölogy," and to have been transformed into modern garb through the influence of Louis Agassiz and his students. In both the "principles" and the "phylum" courses, the method of instruction by "types" has been utilized; but in one case the type illustrates principles, while in the other it shows the morphology and physiology typical of a given phylum.

Recent discussion of methods of teaching General Zoölogy has largely centered upon the relative merits of these two systems, and

has been influenced by certain extreme departures in the attempt to teach principles. Another influence that is being felt is the "Project Method" which has been developed in many high school textbooks. While much is claimed for the Project Method, it seems to be the opinion of most college teachers that the product of the high schools in which this method flourishes is not such as to inspire full confidence in it, whatever may be the current educational theory of the learning process. It may be that the Project Method is the method of the future; but it has not yet arrived in the colleges, and the writers of the present volume have yet to be convinced that good teachers are not principally "born" and relatively little "made," when it comes to instruction of a serious intellectual content. Good teachers arouse the interest of their students, and to be a good teacher one cannot be forever thinking how it is done, else "the letter killeth." When all is said, intellectual work is for the intellectually competent; and, whatever may be the present population of our colleges, one questions whether the Project Method does not tickle the incompetent into temporary activity more often than it stimulates the competent to the work necessary in sustained intellectual effort.

This leads one to consider how a textbook of college Zoölogy should be written; whether it should give the student what he thinks he wants to know and can obtain in a way that takes little effort; or give him what he must know in order to understand something of the subject. The authors incline to the belief that college and university instruction must have a certain regard for the existing organization of subject-matter, for example, for Zoölogy as conceived by zoölogists. As to phraseology, they have attempted to write clearly, but not with undue simplification of vocabulary or expression. It is part of a college training to learn how to read and understand writing that is understandable by educated adults. The only way to learn this is to read such writing. It is better for a student to find places in a textbook a bit difficult than to find it all easy. Whether the authors have succeeded in their attempt to write on a level above primary English, without using a style that is hopelessly beyond those for whom it has been intended, others must say. They profess only the intention.

To a certain extent they have been influenced by the idea that is back of the Project Method. The senior author has always been conscious that such teaching of General Zoölogy as he has done effectively has been largely influenced by a sense of the "humanistic" aspects of the subject. The broader aspects of this "Humanism" of

science have been discussed in a popular volume.¹ Zoölogy is full of human interest—not merely bread-and-butter interest, but interest that may be dignified by the term “humanistic.” This is better developed individually by the teacher than formally in a textbook, since its effect upon the student depends so much upon the conviction of the teacher. On the other hand, the approach to Zoölogy through a study of vertebrate structure and physiology, as in the present work, recognizes the desirability of introducing the subject by means of the facts most familiar and interesting to the student. These are to be found in the body of a familiar animal and in the student’s own body. To begin with the frog is to begin with man, since all vertebrates are so much akin in structure and function. The purpose of the first half dozen chapters is to review the knowledge of human anatomy and physiology that should be part of the training of every high-school graduate, although such is not the case. With this accomplished, and, one hopes, with interest aroused by the human problems involved, the facts and principles of animal life are presented in the formal manner that is current in most textbooks. The “project” in the first part of the work is to teach the student something of the principles of Zoölogy as illustrated in his own type of animal body; and the “project” in subsequent chapters is to teach him how other animal bodies may be compared with his own and to impart some of the many interesting facts about animals. If many of these facts do not interest him, the authors believe he is hopeless. In the final chapters on Development, Genetics, and Evolution, there is a return to more human problems. Here again, the attempt is made to state the facts and principles as clearly and fully as space permits, in the conviction that the origin of the individual and of the race, and the mode of inheritance are of such compelling interest that the teachers’ energy should be directed toward clear presentation of facts and problems, rather than toward overworked schemes for stimulating intellectual laggards. This smacks of a take-it-or-leave-it doctrine in teaching; but we take it or leave it all our lives, and perhaps the principal trouble with college teaching is that we do not make our students feel that college work is a serious enterprise.

As it stands, the present volume represents a temporary crystallization of the course in General Zoölogy as developed in the University of Missouri, although it contains more than the authors are able to offer in a course extending through but one semester. In the

¹ Curtis, W. C., “Science and Human Affairs.”

Laboratory Directions,² designed to accompany the present volume, it was possible to include work upon flatworms, mollusks, and echinoderms. These have been omitted from the text, since it is obviously impossible to deal so largely with principles and at the same time present types of all the phyla. A chapter upon the History of Zoölogy has been omitted in favor of the inclusion of historical references in connection with special topics, since it is the authors' experience that historical chapters are not very effective with students.

In general, the aim has been to include the substantial body of well-established facts concerning the structure and functions of the animals described and to avoid undue inclusion of very recent details, however interesting. The authors hope that the book is not out of date in regard to recent biological investigation, but they have not tried to make it so "up to the minute" that it would soon be found to contain premature conclusions from very recent work. Such details are always better left to the teacher as a means of vivifying his instruction. For example, it is well to explain in a text the salient facts of "endocrine secretion," but not to include very recent extensions that have not been verified. It has been assumed throughout that the laboratory work of the course should be definitely related to lectures and text, and not given as though it were a separate course, as is done in some institutions. The authors' view of laboratory study has been discussed at some length in the Remarks to Instructors as printed in the Laboratory Directions. It is the belief of the authors that a textbook should contain a fundamental body of subject-matter that is correlated with the laboratory work and that may be extended by lectures at the discretion of the teacher. If laboratory work means anything, it should mean some measure of first-hand contact with the facts. On this foundation the text becomes intelligible, and on the basis of laboratory study and text should rest the lectures and other oral discussion. The trouble with "principles" textbooks is that they have no foundation in accounts of representative types of animals; and the trouble with "phylum" textbooks is that they have no space for an outline of principles upon which the teacher can build his own superstructure.

The junior author is primarily responsible for the chapters on Metabolism, Irritability, the Cells of Vertebrates, and Genetics, and has collaborated, by critical editing and by advising, throughout the preparation of the remaining chapters as originally projected or written by the senior author. It is hoped that this united effort has

² Curtis, W. C., and Guthrie, M. J., "Laboratory Directions in General Zoology."

resulted in a better textbook than could otherwise have been produced.

It is impossible, in a work of this nature, to acknowledge all the sources from which assistance has been received. There are the more remote influences, such as the authors have acknowledged in the dedication, and those of former colleagues, including G. S. Dodds and George Lefevre. The entire manuscript, as written before the final revisions, was read critically by Professor E. A. Andrews. Others who have read certain chapters are R. H. Wolcott, E. A. Martin, F. L. Hisaw, and J. A. Dawson. Thanks are due to the authors' colleagues in the department at the University of Missouri, who have collaborated in other ways, and to George T. Kline and Helen Woelfel, biological artists. Other acknowledgments of figures and of permission to use figures appear in the legends.

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CHAPTER 1

INTRODUCTION

This is your introduction to a book which is written to help you gain an understanding of the science of animal life. Perhaps you are wondering whether you need or want this information and why such subject matter forms a part of a college curriculum. Your course of study will usually include three kinds of material—tool subjects, such as composition and speech training in various languages, which aid you in gathering or imparting ideas, or mathematics and logic, which offer training in reasoning and the use of abstract ideas; technical subjects in which you can acquire the professional training which will aid you in earning a livelihood when college days are over; and cultural subjects in which you become better acquainted with your social heritage, the rich background of man's artistic contributions in literature, music, and the arts and his intellectual attainments in the fields of religion, philosophy, and science. In this book you will find a general survey of the facts and theories which constitute a particular branch of science.

It is sometimes said that we live in an age of science because so many of our activities are made easier or even possible by the applications of science. The automobile, the airplane, the radio, and the movies are accepted parts of our lives, carrying us literally and figuratively over all the world, increasing our information, and adding to the pleasure of our existence. Most of us probably consider inevitable and not particularly surprising the widespread use of air-conditioning and television which we are told to expect in the not distant future. So accustomed are we to turning a switch and receiving in return anything from a slice of toast to the sound of an orchestra conducted by Toscanini that we forget our indebtedness to the basic knowledge which has been applied in countless ways.

From agriculture, as from industry, we receive indirectly the fruits of science. Crop rotation as well as erosion control saves the soil. Domesticated animals are improved with respect to egg or milk production. Disease-resistant grains are found, and new types of

fruits and vegetables are propagated. The experiment station is a recognized part of colleges of agriculture throughout our country.

The life-span of man has been increased by the applications of science which we find in the practice of medicine. Against polluted foods and against the spread of disease we have a measure of protection undreamed of a hundred years ago. No longer do plagues bring terror to a district, although diseases such as influenza and infantile paralysis remain unconquered. With the public becoming conscious that venereal diseases can and should be cured, we are entering a period when protection may be extended against these enemies of society. Preventive measures against smallpox and typhoid fever are almost universally used, and inoculations to prevent other diseases or aid in their cure have a wide acceptance. Penicillin, the sulpha drugs, and streptomycin are recent contributions of science to the control of disease. The study of the cancer problem is discussed frequently in the public press and is an excellent illustration of the way in which basic scientific investigation may be applied in the attempt to make our health more secure.

Many other examples of applied science will occur to you. What, exactly, is science? If you consult a dictionary, you will find that the word science is derived from the Latin *scientia*, meaning knowledge. In modern usage, science is knowledge gained by observation and reasoning; it is factual information, correlated and systematized. One of the most important things that any student of elementary science can learn is what is meant by the *method of science*. This method is not the private property of scientists but has wide application by anyone who will understand and use it.

The knowledge which we call science is based upon facts. A *fact* is the real state of things, as distinguished from a belief. How do we determine what is a fact? By observation, by the use of our sense organs. Science begins with sense perceptions. We see that water changes to vapor as it boils; we feel the increasing temperature of a wire held in a flame; we hear the call of a bird. Man has made instruments of measurement in order to record his observations quantitatively and to be able to compare them with those of other observers. It is not profitable to argue about where the corn grows tallest or the buildings are highest because both corn and buildings can be measured, and argument fails to alter facts. The point to understand is that, whatever the branch of natural science, observations on things are its raw materials. Wherever possible these observations are recorded quantitatively—things are counted or measured.

The scientist is not satisfied with the things nature shows him in

her own way. His curiosity is aroused by what she reveals, and he wants to know more. Therefore he tries to think of a way to learn her secrets—he plans an *experiment*. Naturalists before the time of Gregor Mendel¹ had observed that, when plants which differed in certain characteristics were cross-pollinated, both types of plant reappeared in subsequent generations. Mendel planned experiments in which he used plants which he had followed for several generations and knew to be true breeding. He made crosses between plants that differed in only one respect, such as color of flower, length of stem, or color of seed. When the offspring of these crosses appeared, he classified them and recorded the number of each kind. After several years Mendel had a considerable number of recorded facts about the occurrence of these different plant characters in the offspring of successive generations. He had the first accurate data about the course of inheritance.

The painstaking accumulation of *data*, the recording of facts, is only the beginning of science. What do the facts mean; do they have any relation to other recorded facts? Mendel studied his data in order to find the meaning of what he had observed during his experiments. He found that he could explain these facts of heredity by assuming the existence of units of inheritance which behaved in definite ways. In other words, he formulated in his thinking a *hypothesis* which correlated the facts which he had observed. A hypothesis is not regarded as a final explanation. It is subjected to the most rigorous tests that can be devised. If it stands these tests, it is more highly regarded as a correct generalization, one which will render understandable all facts similar to those upon which it is based and one by means of which predictions can be made. Thus, Mendel's generalizations about heredity have been confirmed in a great variety of crosses and have, therefore, changed in status from hypotheses to *laws* or *principles* of heredity. If we are acquainted with these principles, we can predict what will happen when breeding experiments are performed.

The method of science, then, uses the facts of nature as they can be verified by all competent or trained observers. When these facts are recorded, they are analyzed by logical processes of thought, and a generalization which correlates the specific, separate facts is proposed. This generalization, or hypothesis, is then tested and if found unsatisfactory is discarded. When a hypothesis, or theory, has been refined until it seems to be entirely adequate to explain a large body of facts and to serve as a basis for prediction, it becomes known as a

¹ See p. 165 for additional information about Mendel's work.

principle or law. But no scientific principle is beyond criticism; if new facts which cannot be correlated by its statement are discovered, the principle must be revised or discarded.

Science is a slave to the real state of things; truth is its taskmaster. And, because scientists are human beings, they must be constantly on guard lest prejudice or other emotional vices creep unrecognized into the path of rational thinking. The material that is presented to you in this book has been gathered by hundreds of men and women trained in the techniques of observation and logical thinking. It is necessarily summarized without reference, in most cases, to names or personalities, but it is hoped that your teachers will tell you at times some of the fascinating human-interest stories about scientists and their work.

What can you as an individual in a democratic society gain by an understanding of the method of science? You will find that the method of science leads to the accumulation of exact information which is subject to confirmation by any competent observer. It will perhaps occur to you that this accuracy of basic information is responsible for the steady progress of science and the reliability of its applications. Propaganda, or attempted distortion of facts, is no part of scientific procedure. What would be the result of the application of the scientific method to the problems of social organization, of government, and international relations? What would happen if the "diseases" of our social system were analyzed in an unprejudiced way by competent specialists who were then permitted to conduct carefully planned experiments in order to determine what treatment was most effective? We live in an age of science, surrounded by the material benefits of sound observational and experimental practices. Will the time come when we extend these sound practices in the obvious way and reap their benefits in a greater social security? It will come when great numbers of you take an understanding of the scientific method from your college classrooms and apply it to the problems which confront you as citizens in a democracy.

It is sometimes said that science is an enemy of society. When through the utilization of some scientific principle it becomes possible to make something by means of machinery instead of by human beings, workmen lose their jobs. And when such improvements in methods are occurring simultaneously in many fields, this technological unemployment becomes an important social problem. Instead of arranging the required hours of work by man so that more men work fewer hours, with consequent employment for greater numbers and greater leisure for all, the tendency is for a few to work long hours and many to work

not at all. Does this disastrous result suggest that machines should not be made, that science should not be applied? The slaughter of man in automobile traffic is one of the more appalling aspects of modern life. Would you be willing to argue that automobiles should never have been built? Advances in the chemistry of cellulose, a compound present in plants and abundantly available for use, have made possible the manufacture of artificial textiles and dozens of articles in daily use, as well as the development of high explosives. Because men have used these explosives to blow one another to bits, would you say that the chemistry of cellulose should never have been studied? Your generation will see either the solution of the problem of how to control the energy which scientists have released by splitting the nucleus of the atom or the end of civilization as your parents knew it. Does anyone argue in his fear of disaster from the unscrupulous use of the atomic bomb that scientists should not have tried to unlock this storehouse of energy which could be applied with almost unlimited benefits to mankind? No, science is not an enemy of society except as man perverts its contributions. And there are perversions less conspicuous than those mentioned but none the less dangerous. In much advertising we find a completely unwarranted use of "science says" or "science shows" to lend support to fantastic statements. The thoughtful person will ponder these matters.

Now we must begin to tell you what this book is really about. Science is knowledge gained by observing and reasoning. It is divided on the basis of the source of the observations. Thus, in the *social sciences* we have the knowledge gained by the study of man in his social relations. In the *natural sciences*, on the other hand, we find two different types of information. First, in the *physical sciences*, such as astronomy, physics, chemistry, and geology, knowledge of man's non-living surroundings is accumulated. Second, in the *biological sciences*, botany, zoölogy, and psychology, knowledge of living things is sought.

Before we go farther, you should perhaps be told that you will find many words that will be new to you. Each branch of science has its special vocabulary, just as every type of industry or sport has its own list of technical terms. These words will be defined the first time they are used, and many of them will be found in the glossary at the end of the book. Learn to spell these words, to understand their meanings, and to use them. You will enrich your vocabulary as a cultured individual, and you will help yourself in learning the material that is presented in this book. You learn a new vocabulary every time you learn a new game or become a "fan" of some different

sport. Be coöperative; help yourself and your teacher by learning the vocabulary of biological science.

Biology is the science of living things, both plants and animals. *Botany* is the science of plant life. *Zoölogy* is the science of animal life. We observe different aspects of animal life, and each branch of zoölogy has its name. When we study the structure of animals or find the parts of which they are composed, we call our knowledge *morphology*. *Physiology* is the study of function, or the ways in which the parts of animals work. *Embryology* is the study of the development of an individual, the changes through which a fertilized egg passes from its embryonic stages to the adult form. *Genetics* is the study of heredity and variation. *Taxonomy* is the study of the classification of animals into groups on the basis of structural similarity. *Ecology* is the study of animals in relation to both the living and the non-living constituents of their environments, or surroundings. *Zoögeography* is the study of animal distribution on the earth's surface at any particular period. *Paleontology* is the study of animal distribution on the earth's surface from the distant past to the present in successive geologic periods. *Organic evolution* is the study of racial history in contrast to individual development.

Before you have finished reading this book, you will have had the opportunity to learn many things in these several fields of zoölogy. We are going to begin by describing the structure and function of the vertebrates, or animals which have a backbone. You are a vertebrate and have, therefore, a certain degree of familiarity with the facts to be presented. This should help you to orient yourself in this new course.

Earlier in this chapter science was listed as a cultural subject. It is as such that we wish to present the science of zoölogy. The theories of biology have made a deep impression on man's thinking, his literature, and his social philosophy. No better illustration can be cited than the Theory of Natural Selection, proposed by Darwin to account for organic evolution. Laws have been passed to suppress it, churchmen have debated its merits, and wars have been justified by its use. In most cases exact information about the material correlated by this theory has not been used by those who would discredit it. They have not understood that the test of a theory is a very simple one: it must explain facts which can be observed. If any theory does that, no legislation, no debate, and no misuse can contribute to its downfall. With the information to be gained from this book you will be in a better position to accept or reject on their merits many ideas about biology that you will come in contact with outside the classroom.

You will be more competent to judge the soundness of social legislation supposedly grounded in biological principles. And, if you are going to be a farmer or a physician, what you learn here will be found basic to the applied sciences which are to be your techniques. No matter what your post-college days hold we hope that your course in zoölogy will serve to link man's past attainments in this field of research with the progress you can follow year by year throughout your life.

BOOKS OF GENERAL INTEREST TO STUDENTS IN SCIENCE

- "The book of bird life." A. A. ALLEN. The Van Nostrand Co., New York.
- "On the trail of ancient man." R. C. ANDREWS. G. P. Putman's Sons, New York.
- "Galapagos, world's end." C. W. BEEBE. G. P. Putman's Sons, New York.
- "Beneath tropic seas." C. W. BEEBE. Blue Ribbon Books, New York.
- "Jungle peace." C. W. BEEBE. Modern Library, New York.
- "Madame Curie." EVE CURIE. Doubleday, Doran & Co., Inc., Garden City, New York.
- "Pierre Curie." MARIE CURIE. The Macmillan Co., New York.
- "Voyage of the Beagle." CHARLES R. DARWIN. Everyman's Library, Dutton & Co., New York.
- "Life and letters of Charles Darwin." F. DARWIN. Appleton-Century Co., New York.
- "Microbe hunters." P. H. DE KRUIF. Blue Ribbon Books, New York.
- "The frog book." MARY C. DICKERSON. Doubleday, Page & Co., New York.
- "Reptiles of North America." R. L. DITMARS. Doubleday, Page & Co., New York.
- "Birds of New York." (Illustrated by Fuertes.) E. H. EATON. University of the State of New York, Albany, New York.
- "Animals looking at you." P. EIPPER. The Viking Press, New York.
- "Book of insects." J. H. FABRE. Tudor Publishing Co., New York.
- "Crucibles; the lives and achievements of the great chemists." B. JAFFE. Tudor Publishing Co., New York.
- "The universe around us." (Rev. ed.) SIR JAMES JEANS. The Macmillan Co., New York.
- "The mysterious universe." (Rev. ed.) SIR JAMES JEANS. The Macmillan Co., New York.
- "The biological basis of human nature." H. S. JENNINGS. W. W. Norton & Co., New York.
- "Green laurels (Lives of the great naturalists)." D. C. PEATTIE. Simon & Schuster, New York.
- "Creative chemistry." E. E. SLOSSON. Appleton-Century Co., New York.
- "The life of Pasteur." R. VALLERY-RADOT. Garden City Publishing Co., New York.
- "Social life among the insects." W. M. WHEELER. Harcourt, Brace & Co., New York.

CHAPTER 2

VERTEBRATE ORGAN-SYSTEMS RELATED TO METABOLISM

If you will think of animals like dogs, various birds, alligators, frogs, and fishes, all of which are vertebrates,¹ you will recall that each is made up of the *head* and *trunk*; in some a neck and tail are present

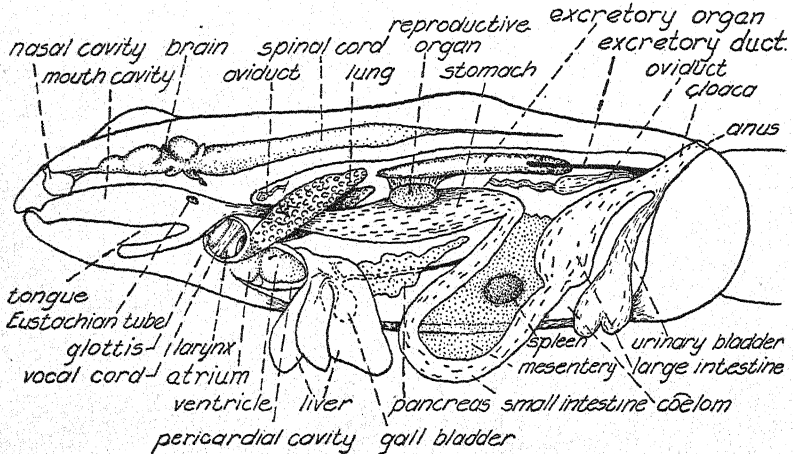


FIG. 1. The frog, shown as if cut in the median longitudinal plane; semi-diagrammatic.

as extensions of the trunk region. Also, in the region of the trunk there are the *appendages*, which are either paired fins or limbs. The *skin*, or integument, forms the outer surface of the body. Derivatives of the skin, such as feathers and hair, are conspicuous characteristics which are used in classifying vertebrates (*cf.* p. 584).

In all vertebrates, except those which walk upright, the head is the most anterior part; that is, it goes first as the animal moves. In correlation with this fact, the eyes and ears, the nostrils, or openings

¹See Chapter 17, pp. 598-642, for a discussion of the kinds of animals that make up this large group in the Animal Kingdom. Notice, especially, the comments on the frog, which is to be referred to frequently.

to the air passages, and the mouth, or anterior opening of the digestive canal, are located in the head region.

The trunk region contains a large cavity without external openings known as the *cœlom*, or body cavity. Here are located the *viscera*, or internal organs, which belong to the several organ-systems to be discussed in this chapter. In adult fishes and frogs, which have the simplest organization of any of the vertebrates, the single undivided *cœlom* which is found in all vertebrates during their development is

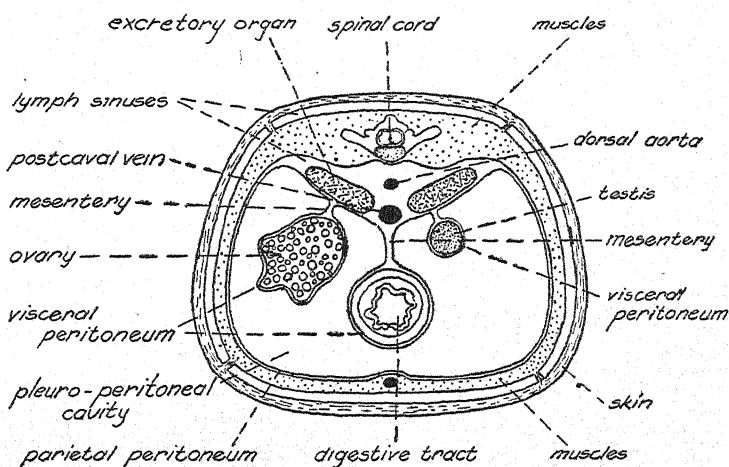


Fig. 2. The frog; a transverse section in the region of the excretory and reproductive organs. The specimen is shown as a male on one side and as a female on the other; diagrammatic.

separated into the *pericardial cavity* and the *pleuro-peritoneal cavity* (Fig. 1). The pericardial cavity contains the heart. The pleuro-peritoneal cavity, which is frequently referred to as the *cœlom*, contains the lungs and other organs. If a transverse section through the trunk of a frog is examined (Fig. 2), it will be noted that parts of the digestive tract, for instance, are suspended and held in place by *mesenteries*, which are made up of two layers of the *peritoneum*, a thin cellular layer that lines the pleuro-peritoneal cavity and covers the organs extending into it. Mesenteries not only support these organs but also function as bridges by way of which blood and lymph vessels and nerves located between the two layers of cells pass to and from *cœlomic* organs (Fig. 3). Figures 1 and 4 show the arrangement of the organs in the *cœlom* of the frog and will be referred to as separate systems are discussed. The *cœlom* of higher vertebrates is divided into four chambers (Fig. 5). The pericardial cavity surrounds the heart and is

located between the two *pleural cavities*, each of which contains a lung. The pleural and pericardial cavities are located in the anterior part of the trunk in a region known as the *thorax*, or chest, which is protected

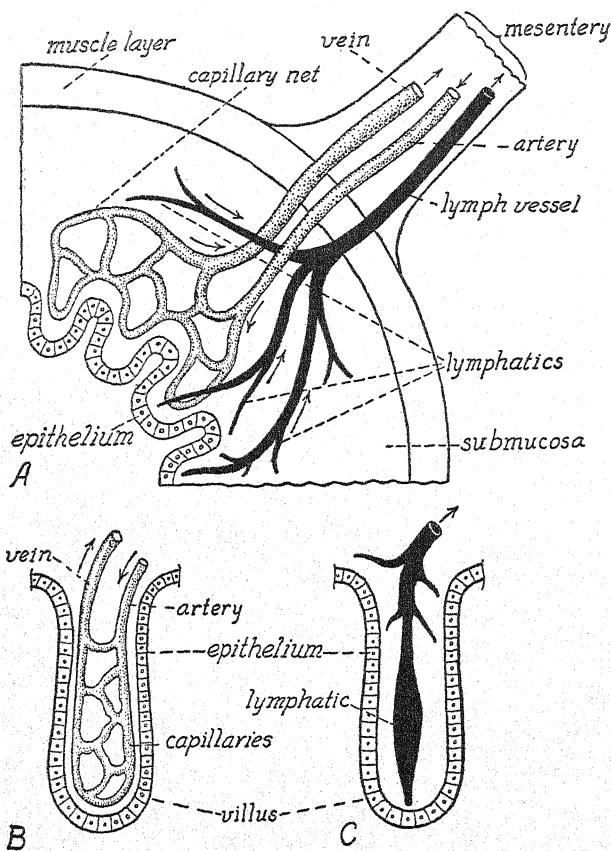


FIG. 3. Blood and lymph vessels in the wall of the digestive tract; diagrammatic. A, a portion of the entire wall. B, capillaries in a villus, or fingerlike projection of the wall of the intestine. C, lymphatic in a villus of the intestine.

Arrows indicate direction of movement of blood and lymph.

by the development of *ribs* and a *sternum*, or breastbone (cf. Figs. 36, 37, and 38, pp. 67, 68, and 69). A muscular partition, the *diaphragm*, separates the pericardial and pleural cavities from the fourth part of the coelom, the *peritoneal*, or *abdominal*, cavity, which is located in the *abdomen*, or posterior part of the trunk.

Appendages are used chiefly for locomotion and are composed of skeletal portions which are jointed together and to which muscles are attached. Although certain reptiles have none and a few other verte-

brates have only a single pair, there are, typically, two pairs of appendages. These are modified in a great variety of ways for locomotion in the water and air and on the land (*cf.* Figs. 487 and 488, pp. 668 and 669).

Another feature of the animals with which we are familiar is that they are individuals, they behave as units. This is true of vertebrates like ourselves as well as of the frog, which is a convenient laboratory

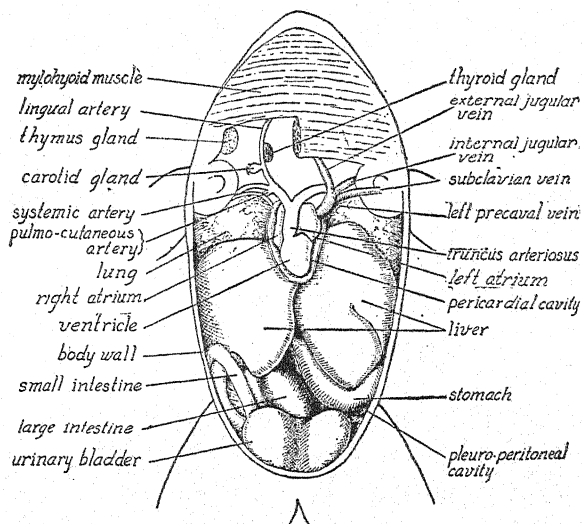


Fig. 4. The coelomic viscera of the frog, from ventral view.

(Redrawn with modifications from G. B. Howes, "Atlas of zoöatomy," copyright, 1902, by Macmillan and Co., Ltd., printed by permission.)

animal for first-hand examination. Brief observation of any individual vertebrate reveals that it is composed of parts, or systems, and that its apparent unity must result from a coördination, a working together, of these systems. Each system is made up of organs that carry on certain functions of the organism. These organs, in turn, are able to do the things they do as a result of the activities of the smaller units, called *cells* (*cf.* Chapter 4), of which they are composed. If, seeking the solution of the mystery of the unity of the individual, we go farther and look within the cells, they are found to be masses of *protoplasm*. It is with an examination of this material that this chapter will continue, because in the organization and activities of protoplasm, of which all living things are composed, we must seek the explanation of the more obvious organization and activities of the animal as a whole.

12 VERTEBRATE ORGAN-SYSTEMS RELATED TO METABOLISM

When we have gained some idea of what protoplasm is and understand that its constituents are being destroyed continually in order to provide the energy necessary for the activity of the individual, it will be obvious that we must consider how this material of life is maintained, how protoplasmic components are replaced. In a complex organism, such as man, the functions of many of the systems are

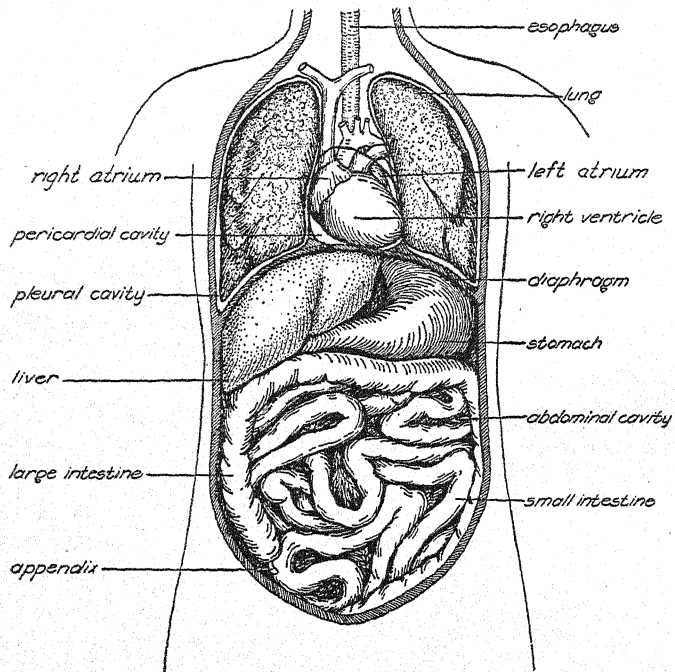


FIG. 5. The coelomic cavities and coelomic viscera of man.

directly related to the necessity of continually building up new protoplasm to replace that which is being destroyed in the flame of life. Other groups of organs enable the individual to rid itself of the waste products produced when protoplasm is destroyed; still others, in movements and locomotion of the organism as a whole, utilize the energy released. The organism is a whole and there are systems responsible for that unity, systems the functions of which are to integrate or co-ordinate the activities of the other systems. Our study of each of the organ-systems of the vertebrate is motivated, therefore, by the necessity for understanding all the parts in order to understand the living whole.

The Nature of Protoplasm

Physical Organization. Although Thomas Huxley, in his famous essay, "On the physical basis of life" (1868), discussed protoplasm as if it were a living chemical compound, and although the phraseology which uses "living matter" as synonymous with protoplasm conveys the same implication, the modern conception is that protoplasm is not a single compound, but a great number of chemical compounds existing together in the form of a *colloidal system*. The term colloid is derived from *kolla*, meaning glue, and is applied to types of liquid substances which do not diffuse through parchment or similar membranes and which, upon evaporation, yield formless masses of material. Such mixtures differ from crystalloid solutions, like those of salt and sugar, which readily diffuse through parchmentlike membranes and yield crystals, or definitely formed masses, when evaporated. Colloidal systems are a subdivision of what are known as *disperse systems*, examples of which are familiar. Whole milk is a disperse system in which small drops of fat, the cream, are dispersed in the watery solution of the other constituents of the milk. If several different substances are dispersed in the same medium, the resulting disperse system is described as polyphasic. The difference between a colloidal system and other disperse systems is the size of the particles which are dispersed. In a colloidal system the particles are too small to be seen with an ordinary microscope but are larger than any save the largest molecules. They range in size from one ten-thousandth of a millimeter in radius down to one millionth of a millimeter. Although such lengths are impossible to visualize, the effect of dividing a given mass into particles of such size can be readily comprehended. If a sphere of material has a radius of 1 centimeter, its total surface will be 12.6 square centimeters. If, however, the same volume of material is contained in colloidal particles of the size range indicated above, the total surface will be between 126 and 12,600 square meters, depending on the radius of the particles. This amazing increase in surface is one of the most significant effects of the colloidal organization of substances, because many important reactions occur at surfaces.

Chemical Constituents. When protoplasm is analyzed chemically, it is found to contain carbon, hydrogen, oxygen, nitrogen, phosphorus, sodium, chlorine, magnesium, iron, potassium, sulphur, calcium, and sometimes other elements, such as silicon, copper, aluminum, manganese, cobalt, boron, iodine, fluorine, and bromine. These chemical

elements are combined to form the three great groups of organic compounds, which are carbohydrates, lipids, and proteins; in addition, there are organic compounds known as enzymes, inorganic salts, and water.

Carbohydrates are compounds of carbon, hydrogen, and oxygen and are so called because the hydrogen and oxygen occur in the ratio of two to one, as in water. Starches and sugars are the most commonly known representatives of the carbohydrates, although cellulose, gums, dextrins, and glycogen are also widely distributed. Carbohydrates of animal protoplasm are made up of structural units known as the simple carbohydrate or monosaccharide groups, which have the empirical formula $C_6H_{12}O_6$. Simple carbohydrates are easily oxidized and furnish the most important source of protoplasmic energy.

The *lipids* are a group of organic compounds which are soluble in ether, chloroform, and benzene but not in water. This heterogeneous group is subdivided into the simple, compound, and derived lipids. Fats and waxes constitute the simple lipids, which are composed of carbon, hydrogen, and oxygen; they contain much less oxygen in proportion to carbon than is found in the carbohydrates. These three elements occur in the form of structural units known as glycerol (glycerin) and fatty acids, which are combined in different ways to give rise to the different chemically pure fats, such as palmitin, olein, and stearin, for which the formulas are $C_3H_5(C_{16}H_{31}O_2)_3$, $C_3H_5(C_{18}H_{33}O_2)_3$, and $C_3H_5(C_{18}H_{35}O_2)_3$, respectively. Natural fats, such as butter, lard, tallow, and cottonseed oil, are mixtures of chemically pure fats. In protoplasm fats are readily oxidized with the liberation of energy, much of which is transformed into heat. The oxidation of fats gives rise to about twice as much heat as the oxidation of carbohydrates. The compound lipids differ chemically from the simple lipids in containing phosphorus and nitrogen, or nitrogen only, in addition to carbon, hydrogen, and oxygen. The structural units in the majority of cases are glycerol, fatty acids, phosphoric acid, and some nitrogen base. Examples of compound lipids are lecithin, which is abundant in the yolks of eggs, and the cerebroside found in the nervous tissue. The derived lipids, as their name suggests, are formed from the simple and compound lipids. Fatty acids belong to this group, as do the sterols which are related to vitamin D, the sex hormones, and the secretion of the adrenal cortex.

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and phosphorus, and sometimes of magnesium and iron. The protein molecule is very large and is composed of structural units known as amino acids, which are organic acids containing nitrogen in an amino group (NH_2). There are twenty-two different amino acids, which are combined in varying amounts and groupings with one another and with other molecules to form the many kinds of proteins. Chemists have not yet succeeded in determining the exact composition of any protein molecule, but by certain methods it is possible to estimate the empirical formulas of some of them. For instance, the approximate formula of fibrin, the protein of clotted blood, is $\text{C}_{645}\text{H}_{1004}\text{O}_{207}\text{N}_{178}\text{S}_5$; that of casein, the characteristic protein of milk, is $\text{C}_{708}\text{H}_{1130}\text{O}_{224}\text{N}_{180}\text{S}_4\text{P}_4$.

Enzymes are substances, many of them proteins, which act as organic catalysts. Catalysts affect the rates of chemical reactions but do not appear among the end products of the reactions. The classic example of inorganic catalysis is the effect of a minute quantity of finely divided platinum in increasing the rate at which hydrogen and oxygen combine to form water. Enzymes are produced in all cells and must be active in the characteristic reactions of protoplasm. Certain cells, known as gland cells, are specialized for the production of enzymes which leave the cells and catalyze extracellular reactions.

The *inorganic salts* of the protoplasmic system include those found in sea water, chiefly sodium and calcium chlorides. *Water* constitutes 60 to 90 per cent of protoplasm and holds the inorganic salts in solution. This watery solution is the dispersion medium for the very finely divided masses of carbohydrates, lipids, and proteins, which are the coexisting dispersed phases. The ionization of the dissolved salts is responsible for the electrical phenomena that are observed in protoplasm.

It cannot be emphasized too strongly that protoplasm is not a living compound but a complex colloidal system. Under the conditions of enormous exposure of surface of the dispersed particles and the intimate associations of these ultramicroscopic masses, the many chemical reactions and the physical phenomena which are characteristic of living cells are made possible. These chemical reactions and physical processes are interdependent, and in normal protoplasm a very delicately balanced equilibrium between such processes gives rise to the visible manifestations that we call life. Life is not a property of any single constituent of protoplasm, of all the components taken together, or of their manner of organization, but is the result of the reactions made possible under the physico-chemical conditions which have just been outlined. As Hopkins puts it, the life of a cell and,

therefore, of an organism "is the expression of a particular dynamic equilibrium which obtains in a polyphasic system" known as protoplasm. The use of isotopes such as heavy hydrogen (deuterium) and N^{15} to tag substances used in nutrition experiments has strikingly demonstrated the constant state of flux in the protoplasmic system.

Distinguishing Capacities of Living Organisms

Living organisms differ from lifeless things in three fundamental respects. These distinguishing capacities are metabolism, irritability, and reproduction. *Metabolism* is the capacity as a result of which protoplasm is built up and destroyed in such a way that the organism lives. The chemical reactions by which these protoplasmic changes occur can be grouped under the headings of assimilation and dissimilation. *Assimilation*, or anabolism, includes those reactions by which suitable materials are built up within cells into the constituent compounds of protoplasm. *Dissimilation*, or catabolism, includes the destructive reactions, chiefly oxidations, which occur in protoplasm and condition the transformation of energy with the production of heat and certain waste products. *Growth* occurs in living organisms when assimilation goes on at a more rapid rate than dissimilation. Organisms grow by the method of intussusception, or growth from within; they differ in this respect from inorganic crystals, which grow by the process of accretion, or the deposition of additional material on the surface of that already present. Metabolic reactions are catalyzed by the enzymes typical of protoplasm and are made possible by its fundamental physico-chemical organization.

Irritability is the capacity as a result of which protoplasm responds to stimuli, or changes in its environment. It is upon this characteristic that the interactions not only between the various constituents of a cell but also between the cells and the systems of an individual depend. It is well known that non-living things react in certain definite ways to changes in their surroundings, as when metals undergo particular amounts of contraction for particular decreases in temperature. The reactions of living organisms, however, involve both chemical and physical factors and are so much more complicated as to be distinctive.

Reproduction is the capacity as a result of which certain parts of organisms detach themselves and, either alone or after union with protoplasm of another organism of the same kind, give rise to a new individual capable of becoming in all essential respects like the parent or parents. Nothing comparable with reproduction is known to occur

among inanimate objects. The capacities of metabolism and irritability enable the individual organism to maintain itself as a living unit. Maintenance of the species is made possible by the capacity of reproduction.

Food

Food is necessary to enable the protoplasmic system to replace those constituents that are constantly being destroyed in dissimilative reactions. In young organisms, food also supplies the materials for growth. Food, therefore, is the source of the raw materials necessary for the normal upkeep of the protoplasmic system, the source upon which assimilation is dependent. Consequently, the nature of food becomes clear. It must contain the elements or compounds needed by the protoplasm for its upkeep and normal functions. If the chemical nature of protoplasm is recalled, it will be evident that food must contain carbohydrates, lipids, proteins, water, and inorganic salts, or materials from which these constituents can be made. Certain organic compounds known as vitamins are also necessary. In addition, atmospheric oxygen must be regarded as a food, since it is essential for the oxidative reactions that are characteristic of dissimilation. The chemical composition of carbohydrates, lipids, and proteins has been indicated.

Early workers in the field of nutrition came to the conclusion that the average adult man needed 400 grams of carbohydrates, 75 grams of lipids, and 100 grams of proteins daily, the so-called "balanced ration." It will be recalled that all carbohydrates are composed of structural units, the simple sugars, of which glucose is the most widespread, and that the lipids have relatively simple and constant structural components. The proteins, however, are built up of amino acids, of which there are twenty-two, combined in many different ways. These twenty-two amino acids have been tested in nutrition experiments to find out which are essential for the growth and maintenance of man. At least eight have been shown to be indispensable food requirements (Fig. 6). These essential amino acids are lysine, tryptophane, phenylalanine, leucine, isoleucine, threonine, methionine, and valine. Man is apparently able to synthesize all the other amino acids; these eight he must have in his food. A so-called complete protein for human diet must contain these essential amino acids. Meat, fish, eggs, milk, and soybeans are such complete proteins.

It is clear that mineral salts are also necessary to maintain the supply of chemical elements used in protoplasmic reactions. These inorganic salts may be present to a greater or lesser extent in the water

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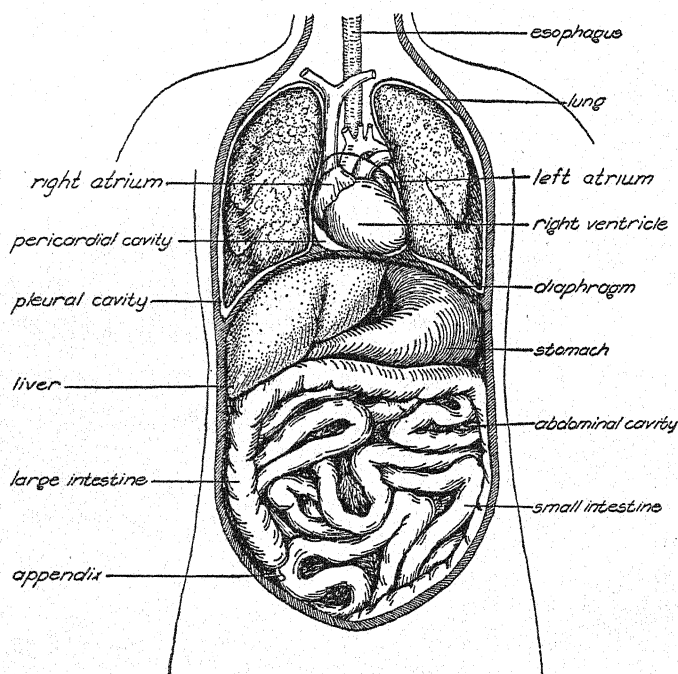


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Enzymes are substances, many of them proteins, which act as organic catalysts. Catalysts affect the rates of chemical reactions but do not appear among the end products of the reactions. The classic example of inorganic catalysis is the effect of a minute quantity of finely divided platinum in increasing the rate at which hydrogen and oxygen combine to form water. Enzymes are produced in all cells and must be active in the characteristic reactions of protoplasm. Certain cells, known as gland cells, are specialized for the production of enzymes which leave the cells and catalyze extracellular reactions.

The *inorganic salts* of the protoplasmic system include those found in sea water, chiefly sodium and calcium chlorides. *Water* constitutes 60 to 90 per cent of protoplasm and holds the inorganic salts in solution. This watery solution is the dispersion medium for the very finely divided masses of carbohydrates, lipids, and proteins, which are the coexisting dispersed phases. The ionization of the dissolved salts is responsible for the electrical phenomena that are observed in protoplasm.

It cannot be emphasized too strongly that protoplasm is not a living compound but a complex colloidal system. Under the conditions of enormous exposure of surface of the dispersed particles and the intimate associations of these ultramicroscopic masses, the many chemical reactions and the physical phenomena which are characteristic of living cells are made possible. These chemical reactions and physical processes are interdependent, and in normal protoplasm a very delicately balanced equilibrium between such processes gives rise to the visible manifestations that we call life. Life is not a property of any single constituent of protoplasm, of all the components taken together, or of their manner of organization, but is the result of the reactions made possible under the physico-chemical conditions which have just been outlined. As Hopkins puts it, the life of a cell and,

therefore, of an organism "is the expression of a particular dynamic equilibrium which obtains in a polyphasic system" known as protoplasm. The use of isotopes such as heavy hydrogen (deuterium) and N^{15} to tag substances used in nutrition experiments has strikingly demonstrated the constant state of flux in the protoplasmic system.

Distinguishing Capacities of Living Organisms

Living organisms differ from lifeless things in three fundamental respects. These distinguishing capacities are metabolism, irritability, and reproduction. *Metabolism* is the capacity as a result of which protoplasm is built up and destroyed in such a way that the organism lives. The chemical reactions by which these protoplasmic changes occur can be grouped under the headings of assimilation and dissimilation. *Assimilation*, or anabolism, includes those reactions by which suitable materials are built up within cells into the constituent compounds of protoplasm. *Dissimilation*, or catabolism, includes the destructive reactions, chiefly oxidations, which occur in protoplasm and condition the transformation of energy with the production of heat and certain waste products. *Growth* occurs in living organisms when assimilation goes on at a more rapid rate than dissimilation. Organisms grow by the method of intussusception, or growth from within; they differ in this respect from inorganic crystals, which grow by the process of accretion, or the deposition of additional material on the surface of that already present. Metabolic reactions are catalyzed by the enzymes typical of protoplasm and are made possible by its fundamental physico-chemical organization.

Irritability is the capacity as a result of which protoplasm responds to stimuli, or changes in its environment. It is upon this characteristic that the interactions not only between the various constituents of a cell but also between the cells and the systems of an individual depend. It is well known that non-living things react in certain definite ways to changes in their surroundings, as when metals undergo particular amounts of contraction for particular decreases in temperature. The reactions of living organisms, however, involve both chemical and physical factors and are so much more complicated as to be distinctive.

Reproduction is the capacity as a result of which certain parts of organisms detach themselves and, either alone or after union with protoplasm of another organism of the same kind, give rise to a new individual capable of becoming in all essential respects like the parent or parents. Nothing comparable with reproduction is known to occur

among inanimate objects. The capacities of metabolism and irritability enable the individual organism to maintain itself as a living unit. Maintenance of the species is made possible by the capacity of reproduction.

Food

Food is necessary to enable the protoplasmic system to replace those constituents that are constantly being destroyed in dissimilative reactions. In young organisms, food also supplies the materials for growth. Food, therefore, is the source of the raw materials necessary for the normal upkeep of the protoplasmic system, the source upon which assimilation is dependent. Consequently, the nature of food becomes clear. It must contain the elements or compounds needed by the protoplasm for its upkeep and normal functions. If the chemical nature of protoplasm is recalled, it will be evident that food must contain carbohydrates, lipids, proteins, water, and inorganic salts, or materials from which these constituents can be made. Certain organic compounds known as vitamins are also necessary. In addition, atmospheric oxygen must be regarded as a food, since it is essential for the oxidative reactions that are characteristic of dissimilation. The chemical composition of carbohydrates, lipids, and proteins has been indicated.

Early workers in the field of nutrition came to the conclusion that the average adult man needed 400 grams of carbohydrates, 75 grams of lipids, and 100 grams of proteins daily, the so-called "balanced ration." It will be recalled that all carbohydrates are composed of structural units, the simple sugars, of which glucose is the most widespread, and that the lipids have relatively simple and constant structural components. The proteins, however, are built up of amino acids, of which there are twenty-two, combined in many different ways. These twenty-two amino acids have been tested in nutrition experiments to find out which are essential for the growth and maintenance of man. At least eight have been shown to be indispensable food requirements (Fig. 6). These essential amino acids are lysine, tryptophane, phenylalanine, leucine, isoleucine, threonine, methionine, and valine. Man is apparently able to synthesize all the other amino acids; these eight he must have in his food. A so-called complete protein for human diet must contain these essential amino acids. Meat, fish, eggs, milk, and soybeans are such complete proteins.

It is clear that mineral salts are also necessary to maintain the supply of chemical elements used in protoplasmic reactions. These inorganic salts may be present to a greater or lesser extent in the water

we drink, but the best single source of such materials is milk, which contains potassium, calcium, phosphorus, chlorine, sodium, and magnesium. Iron, iodine, copper, cobalt, boron, and manganese are also known to be required in adequate diets. Wheat, oats, and vegetables grown on soils that are not depleted of their mineral constituents can be used to supply our bodies with such required elements.

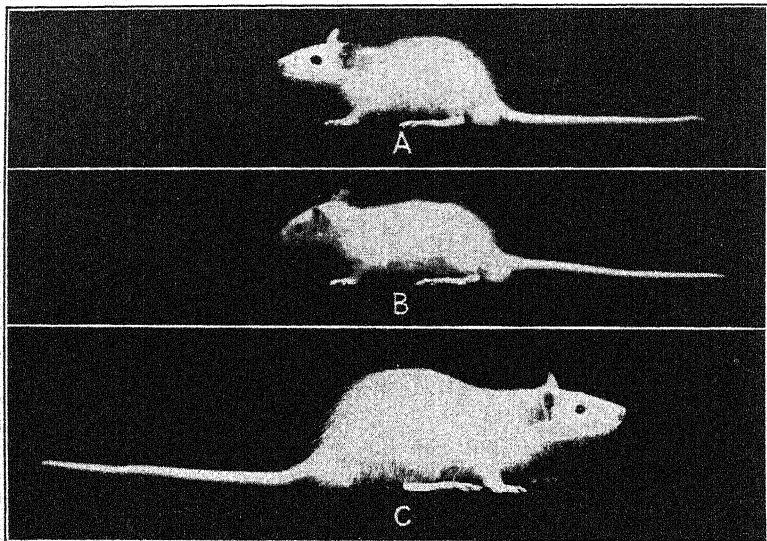


FIG. 6. Rats showing effects of amino acid deficiencies; all are litter mates, 11 weeks old. Rat *A* had protein containing all the essential amino acids but not enough grams of proteins daily; weight, 70 gms. Rat *B* had enough grams of protein daily, but essential amino acids were lacking; weight, 65 gms. Rat *C* had enough protein of good quality; weight, 193 gms.

(Courtesy United States Bureau of Human Nutrition and Home Economics.)

As a result of research since 1910 a considerable list of substances other than the ones previously mentioned has been found to be essential for the growth and maintenance of many kinds of animals, including man, and for a number of bacteria. Such accessory dietary components are called *vitamins*. To be classified as a vitamin for a particular kind of animal, the substance must be one which the animal can obtain only in its food. Certain animals can synthesize a compound which is a specific requirement for growth, or they have bacteria living in their digestive tracts which can synthesize it. Other animals must obtain this same substance ready made in the food they eat, and for them the substance is a vitamin. When a certain com-

pound is said to be a vitamin, it is not to be inferred that all animals must get it in their food. The substance is known to be required by certain specific species which have been tested. It may be known that for certain other species it is not a vitamin, and for many species there will be no information.

When these nutritional substances were first discovered, they were assigned letters for identification. As research continued, it sometimes happened that what had been interpreted as a single substance was found to be a group of substances. Sometimes it turned out that a substance which was reported to be a vitamin was not. With purification of the vitamins, chemical investigators have analyzed their structure and given them chemical names of identification. The more recently discovered vitamins, therefore, have not been assigned letters as names, and the older ones are very often referred to by their chemical names or by a name indicating a major function. In the following paragraphs a brief description of substances currently identified as vitamins, grouped with respect to their solubility in fat or water, will be given. Not all these substances are dietary requirements for man.

The *fat-soluble vitamins* are known as A, D, E, and K. In each case two or more closely related chemical substances have been found to give the effect originally assigned to a single vitamin.

Vitamin A, or to be more exact the vitamins A, is also known as the antixerophthalmic vitamin because in its absence the cornea of the eye in man becomes horny and dry (Fig. 7). Epithelium in other regions may also become horny. Low intake of vitamin A has been correlated with the absence in the retina of a substance called visual purple. The presence of visual purple is essential for normal vision at night. Hence, a deficiency in vitamin A may lead to night blindness. Vitamin A is derived from the typical yellow pigment of plants which is called carotene and which can be transformed into the vitamins A by many animals. Man makes his vitamin A from the carotene in the green and yellow vegetables that he eats or obtains it directly in milk, butter, egg yolk, and fish-liver oils.

The *vitamins D* are also known as the antirachitic vitamin which is essential for the normal deposition of phosphorus and calcium in differentiating bone and in the prevention of rickets (Fig. 8). The vitamin acts by increasing the absorption of calcium and phosphorus in the intestine. Sources of this vitamin are fish-liver oil, butter, liver, and egg yolk. The content of vitamin D in milk, for example, can be increased by exposure to ultraviolet radiation. This hastens the transformation of a vitamin D precursor, ergosterol, to calciferol, which is

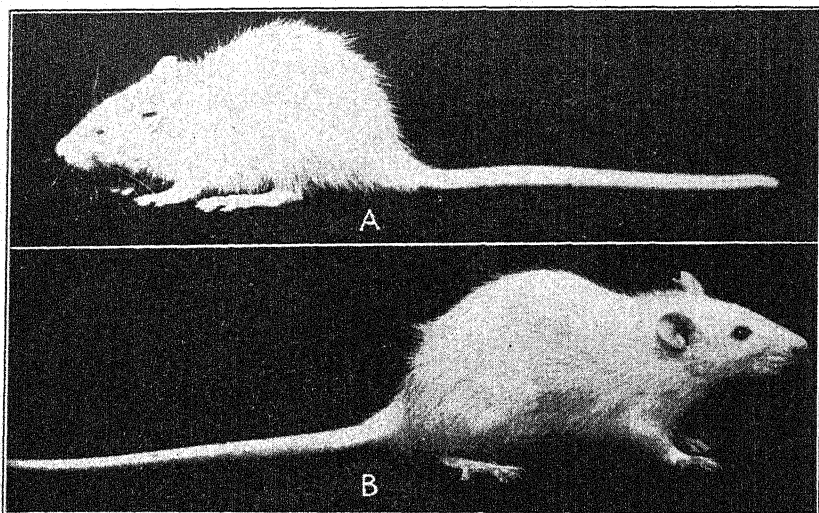


FIG. 7. Rats showing effects of vitamin A deficiency; litter mates, 11 weeks old. Rat A had no vitamin A and has a rough coat, infected eyes, and little vigor; weight, 56 gms. Rat B had sufficient vitamin A and is sleek with bright eyes and is vigorous; weight, 123 gms.

(Courtesy United States Bureau of Human Nutrition and Home Economics.)

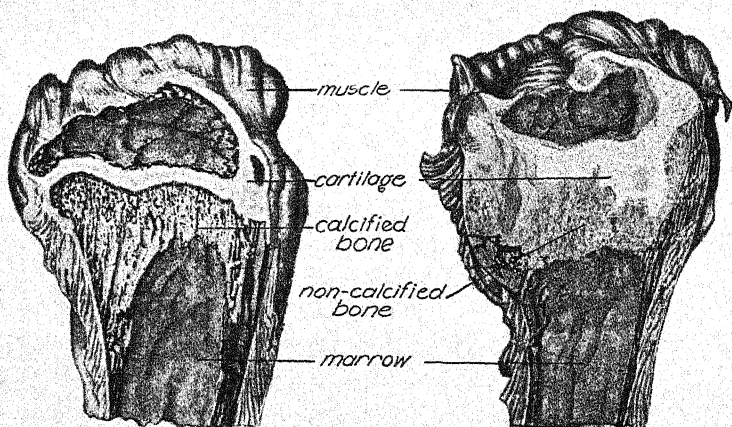


FIG. 8. Bone showing effects of vitamin D deficiency. *Left*, end of tibia from a normal rat. *Right*, end of tibia from a rat with severe rickets resulting from a diet deficient in vitamin D. The relative amounts of cartilage and calcified bone should be noted.

(From C. E. Bills and F. G. McDonald, 1926, *Jour. Biological Chemistry*, vol. 68.)

vitamin D₂. The same reaction apparently occurs in the skin of animals when exposed to sunlight.

The *vitamins E*, known also as the antisterility vitamin, are necessary for normal reproductive function in the rat. The male animal becomes sterile in the absence of vitamin E; the female is unable to maintain the placentas for the nourishment of the embryos, and they are aborted. Neither of these effects occurs in man. An entirely dif-

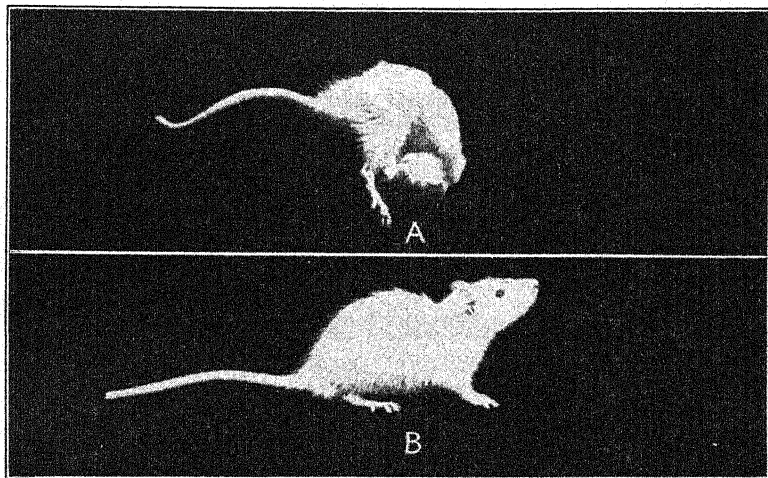


FIG. 9. Rat showing effects of thiamin deficiency; 24 weeks old. Rat A has a paralysis resulting from insufficient vitamin B₁. Rat B is the same individual after having food rich in B₁ for 24 hours.

(Courtesy United States Bureau of Human Nutrition and Home Economics.)

ferent result of deficiency of E vitamins in young animals is degeneration of skeletal muscle or muscular dystrophy. These vitamins are chemically known as tocopherols and are available in green leafy vegetables, whole wheat, and egg yolk.

The *vitamins K* are necessary for the normal coagulation of blood, and the group is called the antihemorrhagic vitamin. In the absence of vitamin K there is a deficiency of prothrombin in the blood (*cf.* p. 99). Mammals usually obtain vitamin K from their intestinal bacteria but may suffer from K deficiency if it is not absorbed normally. Newborn infants sometimes bleed to death because of a lack of vitamin K. However, this vitamin has been synthesized so that it is available for medical use and is routinely administered to expectant mothers in order to guard against hemorrhage in newborn babies. Food sources of vitamin K are green leafy vegetables.

The first *water-soluble vitamin* identified was named vitamin B. It was soon realized that the effects attributed to vitamin-B were the result of a number of different substances, all of which were in some way growth-promoting. In other words, there was no single vitamin B but, instead, what is now often referred to as the B-complex. Nutritional research is still active in this field, and at present at least a dozen entirely different compounds are recognized in this group. We shall

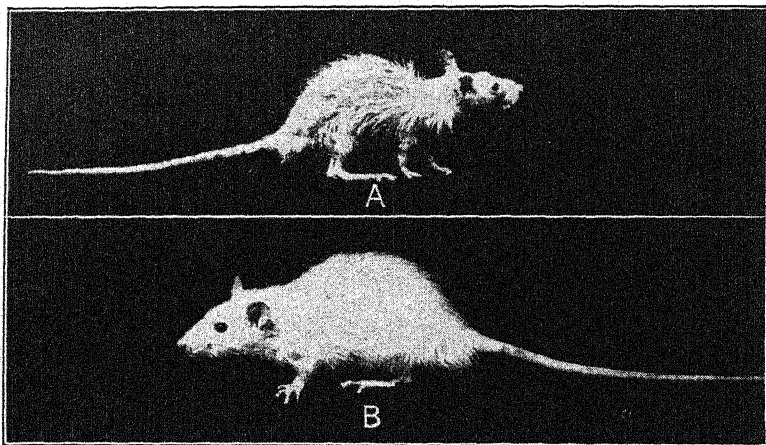


FIG. 10. Rat showing effects of riboflavin deficiency. Rat A has had no vitamin B₂ and is emaciated with much loss of hair; age, 28 weeks, and weight, 63 gms. Rat B is the same individual after having sufficient B₂ for 6 weeks; weight, 169 gms.

(Courtesy United States Bureau of Human Nutrition and Home Economics.)

consider some of the better-understood ones. All have been obtained in crystalline form.

Thiamin, vitamin B₁, or the antineuritic vitamin, in addition to being necessary for growth, protects against the human disease known as beriberi, in which paralysis occurs, and against a similar condition, called polyneuritis, in birds (Fig. 9). Inadequate amounts of thiamin result in loss of appetite with consequent malnutrition. Within the cells this vitamin is essential for carbohydrate metabolism. Thiamin was isolated from rice polishings and finally synthesized in 1936. Yeast, whole wheat, legumes, and lean meat are sources of this protective substance.

Riboflavin, vitamin B₂, or vitamin G is necessary for the growth of many animals, including man, and for the preservation of health in the adult (Fig. 10). Riboflavin deficiency (ariboflavinosis) in man is very widespread and gives rise to soreness at the angles of the mouth

and inflammation of the tongue and cornea. This vitamin occurs in yeast, milk, eggs, liver, and some vegetables. It is required for the synthesis of several enzymes necessary for normal cellular oxidation.

Nicotinic acid, niacin, or the antipellagric vitamin protects man against the disease called pellagra, which was formerly very common in the southern states and was found throughout the country (Fig. 11). Pellagra is characterized by skin lesions, digestive disturbances, muscular weakness, and progressive impairment of the nervous system, often ending in insanity. It was proved to be a dietary-deficiency



FIG. 11. Rats of same age, showing effects of nicotinic acid deficiency. *Right*, rat with pellagra resulting from insufficient niacin; notice the severe dermatitis on the face and legs. *Left*, rat which has had adequate niacin and is healthy and vigorous.

(Courtesy A. G. Hogan, University of Missouri.)

disease in 1914. Since 1937 the medicinal use of nicotinic acid and education regarding proper diet have done much to reduce the incidence of pellagra. Swine and dogs also show similar effects of deficiency of nicotinic acid; the condition in dogs is called blacktongue. This member of the B-complex is abundant in yeast, liver, fresh meat, milk, and egg yolk. Like riboflavin, it is required for cellular oxidation, since it enters into the formation of two enzymes taking part in oxidation in the protoplasm.

Pyridoxine, vitamin B₆, is apparently not a dietary requirement for man, but some other mammals and birds need it. Anemia, dermatitis, and death may result from a deficiency. It is believed to be necessary for the synthesis of fats from proteins in the rat. Yeast, whole cereals, and legumes are good sources of this vitamin.

Pantothenic acid has not been proved to be a vitamin for man but is required for growth by the chick, rat, and dog. Dermatitis follows a deficiency of this substance, and in black rats the hair becomes gray. Yeast, egg yolk, liver, milk, and green vegetables such as broccoli contain pantothenic acid.

Biotin, or vitamin H, is necessary for the growth of various birds but is not a dietary requirement for mammals, in which it is supplied by the intestinal bacteria. The feeding of raw egg white to mammals produces a biotin deficiency in them because the egg white combines with the biotin and renders it ineffective as a vitamin. Diarrhea and dermatitis are symptoms of biotin deficiency. Biotin is found in yeast, egg yolk, and meat.

Choline is another part of the B-complex having specific effects on growth and maintenance in both birds and mammals. It is believed

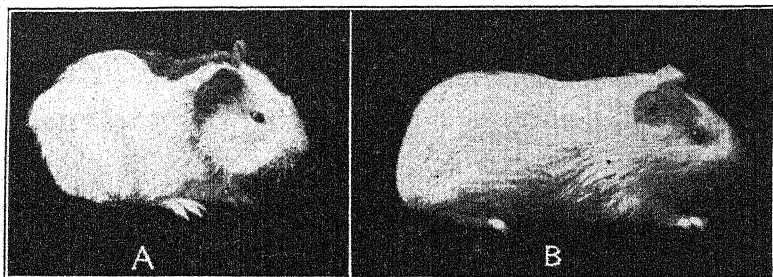


FIG. 12. Guinea pigs of same age, showing effects of ascorbic acid deficiency. Guinea pig A, which had no vitamin C, has scurvy; notice its rough coat and crouched position, which is the result of sore joints. Guinea pig B, which had sufficient vitamin C, is sleek, alert, and healthy.

(Courtesy United States Bureau of Human Nutrition and Home Economics.)

to be necessary for the bio-synthesis of a number of essential compounds, including acetylcholine (cf. p. 86). Deficiency leads to fatty livers and renal hemorrhage in laboratory mammals. *Folic acid*, or vitamin B_c, *inositol*, and *para-aminobenzoic acid* are other factors of the B-complex which are required by birds but are apparently supplied by the intestinal bacteria of many mammals.

Another type of water-soluble vitamin is *ascorbic acid*, vitamin C, or the antiscorbutic vitamin (Fig. 12). It appears to be a dietary requirement for only a very few animals, but man is one of them. Deficiency of ascorbic acid results in scurvy, characterized by bleeding through capillary walls. Citrus fruits and tomatoes are rich sources of this vitamin, and it is abundant in paprika and in the cortex of the adrenal gland.

In the light of modern investigations on the nutritional requirements of animals, it becomes evident that in order to obtain a proper balancing of the diet one must do more than obtain a certain ratio between carbohydrates, lipids, and proteins. It is essential that the proteins eaten contain the amino acids needed by the protoplasm, that

the inorganic elements be present in proper concentrations, and that vitamins be furnished. The abnormal functions of the body conditioned by the inadequacy of food with respect to vitamins and minerals are serious factors in human welfare. On the whole, however, the very numerous cases of borderline malnutrition, predisposing to various diseased conditions and maintaining only a low level of physical and mental efficiency, are of more importance to society as a whole. Every individual should eat abundantly of the "protective" foods.

It is characteristic of the nutrition of animals that they cannot build their foods from the constituent chemical elements but must utilize compounds produced by the protoplasm of other animals or of plants. The protoplasm and the products of metabolism of one type of organism are not ordinarily usable as such by another kind of organism. Therefore, food, in addition to containing the necessary elements which have been discussed, must be utilizable by the animal eating it; that is, it must be possible for the food to be made available for use in the building of the protoplasmic compounds of the animal. The changes which food undergoes before it is assimilated in the body of a vertebrate are well known and will be discussed under the headings of digestion and absorption. These processes occur in the digestive tract, which, together with the digestive glands, is known as the digestive system.

The Digestive System, Digestion, and Absorption

The body of a vertebrate animal is composed of systems of organs which are concerned with activities many of which are related to the necessity of meeting the requirements of metabolism in the individual cells of the organism. It will be our purpose now to consider such organ-systems and their special functions. The *digestive system* is made up of the *digestive tract*, which is a tube, and the attached *digestive glands*, the *liver*, the *pancreas*, and, in many vertebrates, the *salivary glands*. Dissection reveals that the digestive tract is composed of a series of regions sometimes referred to as the digestive organs.

The Regions of the Digestive Tract, and Its Appended Glands: *The Mouth Cavity, Pharynx, and Esophagus.* Beginning at the anterior end of the animal, one finds that the opening of the digestive tract is the *mouth*, which is bounded by *jaws* bearing *teeth* in the majority of vertebrates; in the frog, teeth are found only in the upper jaw and in the roof of the mouth. The mouth opens into the *mouth cavity*, the most anterior region of the digestive tract. Immediately

posterior to the mouth cavity, but with no clearly marked boundary in the adult animal, is the *pharynx*. These two regions, the mouth cavity and the pharynx, will be considered together. They appear to be quite different in the frog and man, since the nostrils of the frog lead directly into the anterior end of the mouth cavity (Figs. 1

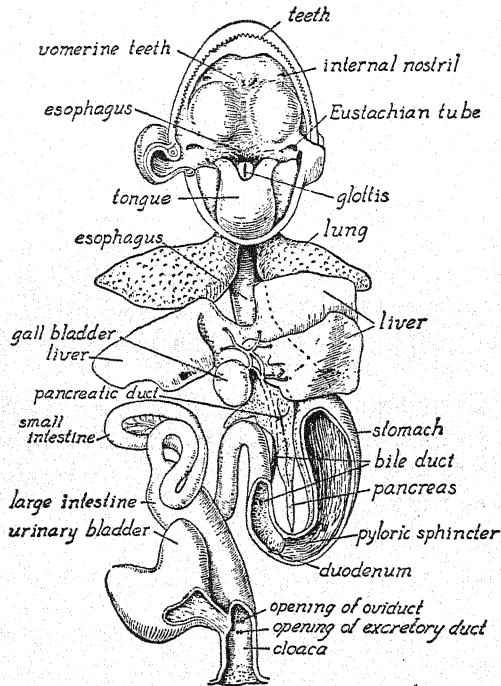


FIG. 13. The digestive tract and appended structures of the frog.

(Redrawn with modifications from G. B. Howes, "Atlas of zoöatomy," copyright, 1902, by Macmillan and Co., Ltd., printed by permission.)

and 13), whereas in man they open into an extensive *nasal cavity* that communicates posteriorly with the pharynx (Fig. 14). However, in the early stages of development of a human embryo, there is a mouth cavity into which the nasal cavities open as they do in the adult frog. As development continues in man, ingrowths from the right and left sides of the mouth cavity of the embryo meet in the midline to form the *hard palate*, which divides the mouth cavity into two parts, the upper of which becomes the nasal cavity. A posterior extension known as the *soft palate* partially divides the pharynx.

The apparent difference in the frog and man in the openings of the *Eustachian tubes*, which lead to the cavities of the middle ears, is un-

derstandable as a result of the division of the primitive combined mouth and pharyngeal cavities (Figs. 13 and 14). These Eustachian tubes are an illustration of the way in which structures become changed both in the history of a group of similar animals and in that of an individual. In primitive vertebrates, such as the fishes, water passes through the mouth cavity and pharynx to the outside by way of a series of openings known as the *gill slits*, near which the gills, or

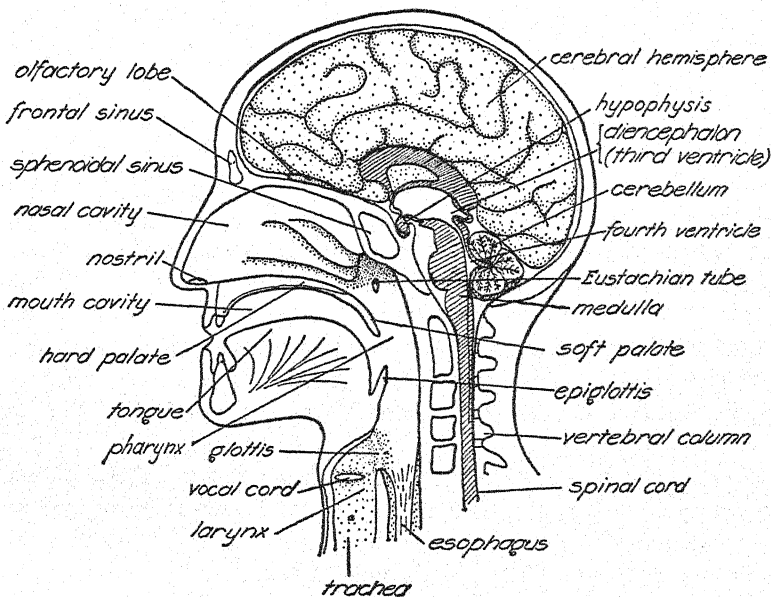


FIG. 14. The human head, shown as if cut in the median longitudinal plane; semidiagrammatic.

respiratory organs, are borne. The gills and functional gill slits disappear in adult vertebrates which possess lungs, but such air-breathing vertebrates always pass through a developmental stage at which gill pouches occur along the sides of the pharynx. Part of the most anterior pair persists and becomes transformed on each side into the cavity of the middle ear and the Eustachian tube.

Two other points of difference in the structures of this region in the frog and man should be noted. The *tongue* of the frog extends backwards, in contrast to the condition in man and many other vertebrates. During development the floor of the mouth cavity becomes thickened to form the tongue, which usually grows anteriorly but may grow posteriorly as in the frogs and toads. The ways in which the tongue can be used are obviously correlated with its structure. In

man three pairs of *salivary glands* (cf. p. 31) secrete saliva, which passes into the mouth cavity by way of ducts. Two of these ducts open near the base of the tongue and can be easily seen. Salivary glands are not present in the frog.

Posterior to the pharyngeal region, the digestive tract becomes a narrow, relatively simple tube, the *esophagus*. The length of this region is correlated with the general structure of the vertebrates. In those with necks and conspicuous thoracic regions, the esophagus is long, since it always connects the parts of the tract that are located in the head with those situated in the cœlomic cavity (Fig. 5). The frog has a relatively short esophagus (Fig. 13).

The Stomach and Small Intestine. The esophagus is continuous with the stomach, which is an expanded portion of the digestive tract variously modified in different vertebrates. In the frog and man the structure of the stomach is essentially the same, but in man its position has been shifted, so that part of the stomach lies almost at right angles to the longitudinal axis of the body (Fig. 5). Although the stomach is relatively short, its inner surface is increased by longitudinal folds in its lining. The posterior extent of the stomach is marked by the *pyloric sphincter*, a muscular ring which, when contracted, separates the cavity of the stomach from that of the small intestine (Fig. 13).

The *small intestine* is a very conspicuous region of the digestive tract because of the length it attains. The length is correlated with the character of the diet, being shorter in carnivorous than in herbivorous vertebrates. This is strikingly illustrated by the change in length from about 20 inches in a tadpole to about 12 inches in an adult bullfrog. Man has about 20 feet of small intestine. The area of the inner surface of the intestine is correlated with its length and is increased by elevations of the lining into fingerlike processes known as *villi* (Fig. 3).

The amount of inner surface in both the stomach and small intestine is extremely important in view of the function of absorption and the presence in the lining layer, the *mucous membrane*, of the glands that secrete the digestive juices, which contain the digestive enzymes. At this point it may be well to consider glands briefly, since many are present along the digestive tract. *Glands* are organs the cells of which build up substances that must be present in order for certain reactions to occur. Such substances are called *secretions* and doubtless are synthesized in the protoplasm of all cells. However, gland cells produce conspicuous amounts of secretions. Glands may be unicellular, as the goblet cells of the intestinal epithelium, or multi-

cellular (Fig. 15). All glands begin their formation on surfaces of the body and usually sink below the surface. In doing so they may form simple *tubular glands* or become flask-shaped to form simple *alveolar glands*, which do not occur in the digestive tract but are found in the skin of the frog. Both types of simple glands may become compound by the formation of out-pocketings along their lengths. The glands related to digestion, and many others, are divided into the secreting portions and the tubes, or *ducts*, by way of which the secre-

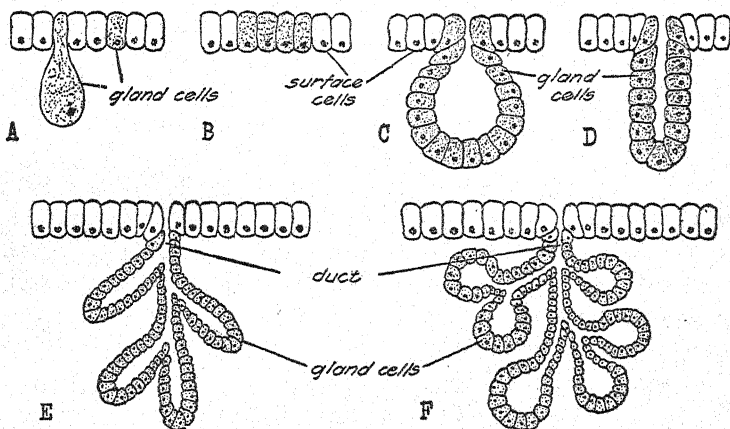


FIG. 15. Diagrams of glands. A, unicellular glands; the one to the left is shown extending below the surface layer of cells. B, a group of gland cells remaining in the surface layer. C, a simple alveolar gland. D, a simple tubular gland. E, a compound tubular gland. F, a compound alveolar gland.

tion passes out to the cavity or surface where it is used. Not all glands possess ducts; those that do not, the ductless glands, will be discussed in another chapter (pp. 55-60). The *gastric glands*, present in the mucous membrane of the stomach, and the *intestinal glands* that occur in the mucous membrane of the small intestine are simple tubular glands. The *liver* and *pancreas* arise as outgrowths from the lining of the intestine and extend into the mesenteries to become conspicuous parts of the digestive system (Figs. 1 and 13). The liver is a compound tubular gland; the pancreas is a compound alveolar gland. These glands retain their connections with the cavity of the intestine by way of the *bile duct* from the liver and the *pancreatic duct* from the pancreas. The ducts are slender tubes, and in the frog they unite before entering the *duodenum*, as the anterior region of the small intestine is called. In man and many other vertebrates, these ducts enter separately.

The Posterior Parts of the Tract. In all vertebrates, the small intestine is continuous with the *large intestine*. Some of the mammals have a blind cavity, the *cæcum*, at the junction of the small and large intestine, but the frog has nothing of the kind. It is the blind end of the rudimentary cæcum that is known as the *appendix* in man (Fig. 5). In some mammals like the rabbit that live exclusively on vegetation, the cæcum is an important storehouse of food, but it probably has no function in other forms. The large intestine is quite short in the frog, but it is conspicuous in man and separated into a *colon* and a *rectum*, which is terminated by the *anus*. In most of the vertebrates, as in the frog, the large intestine is not differentiated into regions. It opens into the *cloaca*, which is a common passageway for substances entering from the kidneys and urinary bladder and for the germ cells from the reproductive organs, as well as for materials that have come through the large intestine (Figs. 1 and 13). The external opening of the cloaca is the anus. When this original common exit chamber is divided into a ventral urino-genital sinus and a dorsal rectum, a new external opening is formed ventrally, and the term anus is retained for the opening through which materials leave the digestive tract.

Ingestion and Egestion. The digestive tract is a canal through which various materials pass. These substances enter the tract by way of the mouth during what is known as *ingestion*, or eating. The method of ingestion varies in different vertebrates. The frog's tongue is extended and withdrawn; an insect is ingested. Other vertebrates with short necks, like ourselves, use the hands to bring food to the mouth; forms with longer necks, such as cats and dogs, ingest directly with lips and tongue.

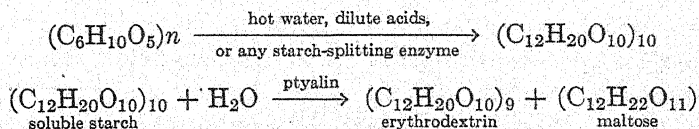
Not all that enters the mouth cavity is food, in the sense that it is usable by the organism, and sometimes an animal does not use what it might on account of abnormal functioning. Unusable or unused material passes through the cavity of the digestive tract without ever really being inside of, or a part of, the animal. Such material is found in the *feces*, or contents of the large intestine, and is eliminated through the anus by the process of *egestion*, or defecation.

Between the time when ingestion occurs through the mouth and egestion through the anus, food materials are passing from one region of the digestive tract to another; the very important processes of digestion and absorption are occurring. These will be considered now as the major functions of the digestive system. In addition, certain muscular activities of the tract related to separating food masses into small pieces, mixing the food with the digestive juices, and passing

the material from one region to the next will be described. The various functions of each particular part of the system will be discussed in sequence, and you should pay careful attention to the correlation between structure and function.

Digestion. *Digestion* is defined as the series of chemical changes which food undergoes in the digestive tract in the presence of digestive enzymes. The great majority of foodstuffs must be chemically changed by digestion for two reasons: first, because the complex molecules cannot leave the digestive tract as such; that is, they cannot be absorbed in order to be distributed to all cells of the body; and second, because the complex molecules cannot be used as such by the protoplasm in replacing its constituents. Since assimilation must occur if an organism is to remain alive, and since absorption must occur before substances can reach the cells where assimilation takes place, the great importance of digestion is apparent. Digestion consists of a series of chemical reactions as a result of which complex molecules are separated into simpler structural units. This essential chemical disintegration must not be confused with the gross mechanical breakdown resulting from muscular activities.

In the mouths of the higher vertebrates the food may be torn apart or ground into fine particles by the teeth, but in lower forms the food is merely held by the teeth and no mechanical disintegration occurs. The frog, for instance, retains food with the teeth until it can be swallowed, and no digestive changes occur in the mouth. However, in man, the sight, the odor, or even the thought of food induces the flow of *saliva*, a digestive juice secreted by the salivary glands. As the food is chewed, it is mixed with the saliva. This results in a softening of the food, which aids in swallowing and also in the initiation of the digestive changes. Although saliva is largely water and mucin, it contains a digestive enzyme known as *ptyalin*, in the presence of which starchy foods are partially digested. Starch, if it has been cooked, enters the mouth in soluble form; if not, it is made soluble by the ptyalin. Soluble starch in the presence of ptyalin reacts with water to form erythrodextrin and maltose, one of the compound sugars. Certain investigators believe the reactions to occur as follows:



This reaction, which is a splitting of the starch and dextrin molecules by the addition of water, continues until the effect of the ptyalin,

which is active only in a neutral or alkaline medium, is halted by the acidity of the juices of the stomach. The food mass, softened by the water and mucin of the saliva, mixed by chewing, and with its starch components partially digested, is carried down the esophagus by the muscular movements known as swallowing. No digestive changes occur in the esophagus; it is merely a passageway.

The food mass is retained in the cavity of the stomach because of the contraction of the pyloric sphincter and is thoroughly mixed with

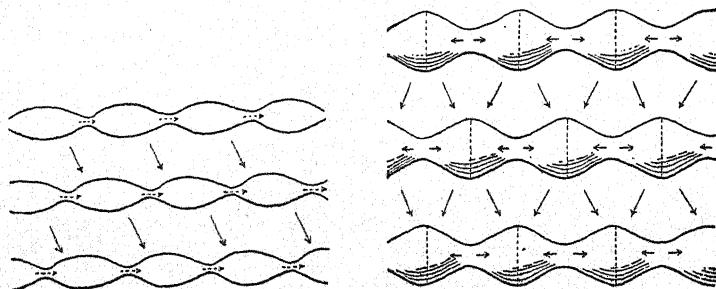


FIG. 16. Peristalsis and segmentation. The drawings on the *left* show a particular region of the small intestine at successive periods during peristalsis. The drawings on the *right* represent a particular region of the small intestine at successive periods during segmentation. Arrows within the tube show the direction of movement of the food contents. Arrows between drawings call attention to movements of the wall of the intestine. The vertical dotted lines in the drawings on the right indicate the places of successive contractions.

the digestive juice of the stomach, which is known as *gastric juice*, by muscular movements of the stomach wall. Gastric juice, secreted by the gastric glands, is strongly acidic because of the presence of hydrochloric acid and contains two enzymes—pepsin and rennin. *Pepsin*, the action of which is dependent upon the presence of the hydrochloric acid (HCl), starts the digestion of some of the protein foods and brings about their disintegration into proteoses and peptones. *Rennin*, which is present chiefly in the stomachs of young milk-feeding animals and is not found in the frog, has a coagulating effect upon milk. As the acidity of the stomach contents increases, the pyloric sphincter relaxes at intervals, permitting the expulsion of the partially digested food mass from the stomach into the small intestine.

The muscular activities of the small intestine are of two types, known as peristalsis and segmentation (Fig. 16). In *peristalsis*, a muscular contraction begins at the upper end of the intestine and passes with wavelike effect toward the lower end. This motion has a

tendency to bring about the movement of the food mass toward the large intestine. *Segmentation*, on the other hand, consists of a series of contractions occurring close together and simultaneously at different levels of the intestine. This results in the pinching of the food mass into segments; and, since these segmentation contractions disappear and reappear at alternate levels, they produce a very thorough mixing of the intestinal contents. Food in the small intestine is acted upon by three digestive juices: *bile*, entering from the liver by way of the bile duct; *pancreatic juice*, coming from the pancreas through the pancreatic duct; and *intestinal juice*, from intestinal glands in the lining of the duodenal region of the small intestine. The reactions of this region occur in an alkaline medium. Bile contains no digestive enzymes and serves chiefly as an emulsifying agent for the fats; thus, fat drops in the presence of bile become divided into very fine droplets, which offer a much greater surface for the activities of the fat-splitting enzyme. Pancreatic juice contains three digestive enzymes: *steapsin*, *trypsin*, and *amylopsin*. *Steapsin* brings about the digestion of the emulsified fats into glycerol and fatty acids. *Trypsin* is the enzyme which splits the undigested or partially digested protein molecules into simpler compounds known as polypeptids. *Amylopsin* continues the digestion of starch, started in the mouth and interrupted in the stomach, and converts starch into maltose, which is a compound sugar. The intestinal juice contains *enterokinase*, *erepsin*, and the sugar-splitting enzymes. Without *enterokinase*, *trypsin* is inactive and has no effect upon proteins. *Erepsin* is the enzyme that finally completes the digestion of proteins into their component amino acids. Of the sugar-splitting enzymes, *maltase* acts upon maltose, or malt sugar; *sucrase*, or *invertase*, upon sucrose, or cane sugar; and *lactase* upon lactose, or milk sugar. The effect of these enzymes is to produce simple sugars, principally glucose, or grape sugar. The final stages of digestion of all foods occur in the small intestine.

The ingested materials that have not been digested are carried by peristaltic contractions toward the large intestine, which is separated from the small intestine by the ileo-cæcal valve. In man, the first part of the food mass enters the large intestine about 4 hours after eating, and the discharge continues for about 2 hours. After being retained in the lower part of the large intestine for from 10 hours to 2 days, this undigested and undigestible material, now known as feces, is egested. The amount of material egested is about 10 per cent of the amount ingested. In the large intestine of some animals there are many bacteria which digest cellulose, a carbohydrate

Regions of Digestive Tract	Digestive Juices	Sources of Digestive Juices
Mouth cavity	Saliva	Salivary glands
Esophagus	None	None
Stomach	Gastric juice	Gastric glands
Small intestine	Bile	Liver
	Pancreatic juice	Pancreas
	Intestinal juice	Intestinal glands
Large intestine	None	None

FIG. 17. The principal

Digestive Enzymes		Foods Changed	End Products
Ptyalin		Starch (carbohydrate)	Maltose
None		None	None
Pepsin (in the presence of HCl)		Proteins	Proteoses and peptones
Rennin		Milk protein coagulated	Paracasein
None		No foods digested; lipids emulsified	None
Amylopsin		Starch (carbohydrate)	Maltose
Trypsin (in the presence of enterokinase)		Proteins, proteoses, and peptones	Polypeptids
Steapsin		Lipids (after emulsification)	Glycerol and fatty acids
Erepsin		Polypeptids (formed from proteins)	Amino acids
Sugar-splitting enzymes	Maltase	Maltose (compound sugar)	Glucose (simple sugar)
	Lactase	Lactose (compound sugar)	Glucose and galactose (simple sugars)
	Sucrase (invertase)	Sucrose (compound sugar)	Glucose and levulose (simple sugars)
None		None	None

facts about digestion.

present in the walls of plant cells, and produce simple sugars from it. Although some of this sugar is absorbed, it must be kept in mind that the bacteria digest this material for their own assimilation, and it is only incidentally that it affords nourishment for the animal harboring the bacteria. Protein substances are putrefied by bacteria in the large intestine of man and give rise to products many of which are toxic, or poisonous. When these are absorbed, they are sometimes built up into non-toxic products before being eliminated from the body by way of excretory regions. Bacteria in the digestive tract also produce substances necessary for the growth and maintenance of many animals (cf. p. 18). Some idea of the great numbers of bacteria present can be had when it is stated that from one-quarter to one-half of the dry matter of the feces consists of bacteria.

In summarizing the essential processes of digestion (Fig. 17), it may be recalled that in animals which possess salivary glands the digestion of starchy carbohydrates may be started in the mouth by the action of ptyalin. This action on starch is continued in the small intestine by the amylase of the pancreatic juice, with the result that the starch is converted into maltose, a compound sugar. The digestion of the maltose and other compound sugars is completed by the sugar-splitting enzymes of the intestinal juice, with the formation of the simple sugars. Protein digestion, initiated by pepsin in an acid medium in the stomach, is continued in the small intestine in an alkaline medium by trypsin of the pancreatic juice and completed by erepsin of the intestinal juice with the formation of amino acids. Lipids are split in the small intestine, after emulsification by bile, by steapsin from the pancreas, and glycerol and fatty acids are produced as the end products of fat digestion. The entire result of digestion is the disintegration of complex food materials into their structural units, which are simple sugars, amino acids, glycerol, and fatty acids. These compounds are thus made available for absorption and assimilation.

Absorption. During the process of digestion, complex food materials are chemically changed to simpler compounds that can be assimilated by the cells. Before assimilation can occur, the simple nutrients must be absorbed from the alimentary canal into the circulating fluids and be distributed to all the cells. *Absorption* may be defined as the passing of simple food compounds through the lining of the digestive tract into the blood or lymph. Between the mucous membrane and the muscular coats of the tract is the submucosa, a region of loosely arranged cells with interlacing fibers. It is in this

region, separated from the digestive cavity by the mucous membrane, that the delicate lymphatics and the thin-walled capillaries that connect arteries and veins are found (Fig. 3). In being absorbed, substances pass through the epithelium of the mucous membrane and into the fluids of these vessels.

Although certain foods, such as glucose, water, and the inorganic salts, require no change before they are ready for absorption, they are not absorbed in the stomach. In the upper part of the small intestine, where the surface of the mucous membrane is greatly increased by folding and, in mammals, by the projection of numerous fingerlike villi, by far the greatest amount of absorption occurs. In man it has been estimated that there are 10 square meters of absorptive surface in the small intestine. Simple sugars, amino acids, and mineral salts pass directly into the blood stream. The fatty acids combine with certain alkaline constituents of the bile to form soaps. In this condition they enter the surface cells of the mucous membrane together with the glycerol. There the soaps are broken down, and the fatty acids recombine with the glycerol to form fat droplets, the presence of which can be demonstrated in the protoplasm of the epithelial cells of the lining of the intestine. This fat passes into the lymphatics of the submucosa. Water is absorbed chiefly in the large intestine.

No satisfactory theory to account for absorption has been formulated. Osmosis, the passing of fluids through a membrane in such a way that concentrations of solutions on the two sides of the membrane tend to be equalized, would account for the passing of water into the digestive cavity to decrease the concentration of the food mass but not for the absorption of water in other regions of the tract. It would account, also, for the passage of digestion products from the tract, where they are very concentrated, into the circulating fluids, which are constantly changing so that equilibrium is not established. However, it has been found that, if the fluid portion of the blood of an animal is introduced into its digestive cavity, this blood serum will be absorbed very soon into the circulating blood, which must have the same concentration. It is evident, therefore, that factors other than osmosis must be considered. In the absorption of fat, the surface cells of the mucous membrane are not passive. The fact that the glycerol and fatty acids are synthesized into fat is evidence of protoplasmic activity. Indications of such activity are not so obvious in the absorption of other substances, but it is safe to say that no explanation will be found satisfactory that does not take into consideration the metabolism and organization of the protoplasm of the epithelial cells.

The Circulatory System and Circulation

Materials which enter the digestive tract and are absorbed from it pass into the circulating fluids, by means of which distribution to all the cells of the body occurs. These fluids, the *blood* and *lymph*, are carried by vessels comprising the *circulatory system*, which is sub-

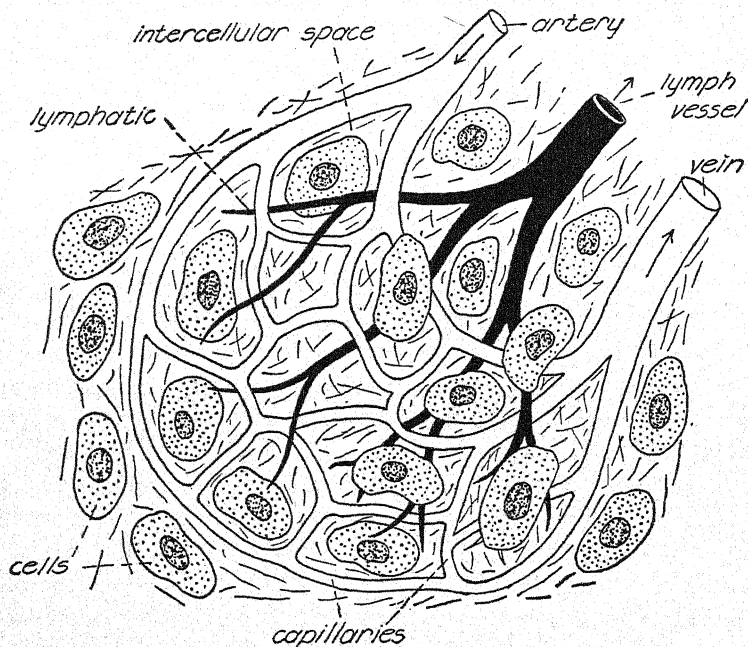


FIG. 18. The capillaries and lymphatics in relation to cells throughout the body; diagrammatic. The arrows indicate the direction of circulation.

divided into the blood-vascular and lymphatic systems, depending on the fluid that is carried.

The Blood-vascular System. The blood-vascular portion of the circulatory system of all except the lowest vertebrates is what is known as a closed vascular system, because the blood is everywhere contained in vessels and does not flow out freely between the cells. Some kinds of animals have open vascular systems, which will be described in later chapters. The chief parts of the blood-vascular system are the same in all vertebrates. There is a differentiated region known as the *heart*, which by contracting rhythmically, beating as we say, forces the blood into the *arteries*, or vessels in which blood flows away from the heart. Arteries divide and redivide as they pass to all parts

of the body and finally end in a network of very thin-walled, small vessels known as *capillaries* and found in all the organs of the body in close association with the cells. The capillaries are also connected with other larger vessels, known as *veins*, through which the blood returns to the heart. The arteries and veins that are seen when a vertebrate animal like the frog is dissected are, therefore, continuous with each other in organs all over the body by way of the capillaries, which are visible when magnified (Fig. 18). Likewise, the heart connects the veins and arteries, so that the blood flows continuously away from the heart through the arteries, into the capillaries, thence into the veins,

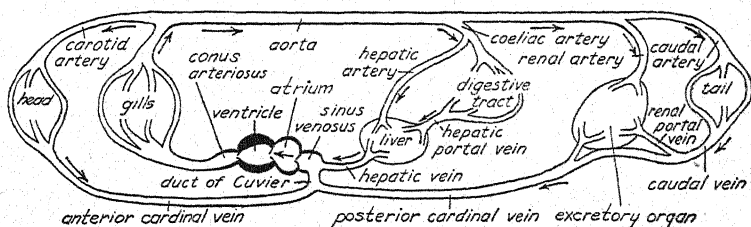


FIG. 19. The circulatory system in a vertebrate having a heart with one atrium and one ventricle, as in elasmobranch fishes; diagrammatic. The arrows indicate the direction of circulation.

and so back to the heart. Although this statement describes a very simplified circuit, such as that in the fishes, it is essentially true for all vertebrates. The differences that exist in the circuits of the different kinds of vertebrates are related to changes that occur in the heart and to changes in some of the larger arteries and veins that supply the respiratory and excretory organs. In the heart of any vertebrate there are valves, between the chambers and at the openings of the large blood vessels, that determine the flow of the blood in a given direction. Such valves are thin extensions of the lining of the heart (Figs. 22 and 23).

If one compares the circulatory systems of a fish (Fig. 19) and a frog (Figs. 20 and 21), the important change to be noted is that the heart of the frog has two atria and one ventricle, whereas that of the fish has only one atrium and one ventricle. Blood leaves the heart by way of a large artery in both forms. In fishes blood is carried first to the capillaries of the gills, or respiratory organs, and thence to other parts of the body. In the frog, however, the *truncus arteriosus* divides right and left, and on each side there are three branches (Fig. 22). Of these, the *pulmo-cutaneous arteries* supply blood to the lungs, or respiratory organs, while the *carotid* and *systemic arteries* carry

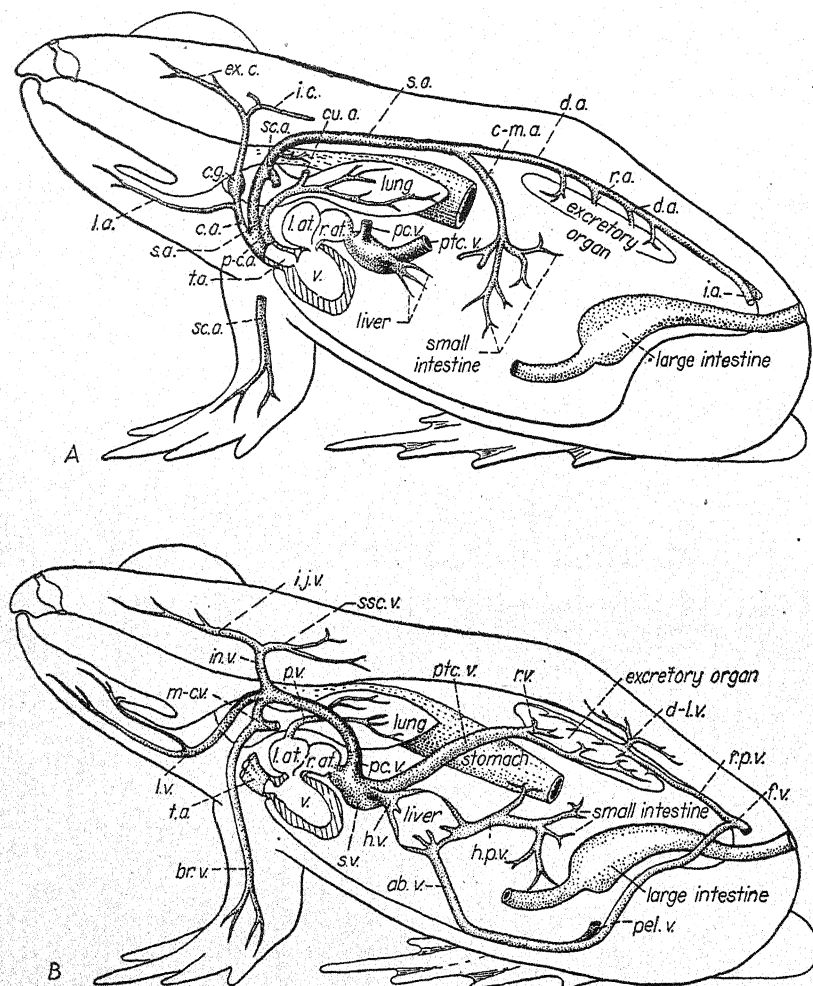


FIG. 20. The circulatory system of the frog; from lateral view. *A*, arteries. *B*, veins. *ab. v.*, abdominal vein; *br. v.*, brachial vein; *c. a.*, carotid artery; *c. g.*, carotid gland; *c. m. a.*, coeliaco-mesenteric artery; *cu. a.*, cutaneous artery; *d. a.*, dorsal aorta; *d. l. v.*, dorso-lumbar vein; *ex. c.*, external carotid artery; *f. v.*, femoral vein; *h. p. v.*, hepatic portal vein; *h. v.*, hepatic vein; *i. a.*, iliac artery; *i. c.*, internal carotid artery; *i. j. v.*, internal jugular vein; *in. v.*, innominate vein; *l. a.*, lingual artery; *l. at.*, left atrium; *l. v.*, lingual vein; *m. c. v.*, musculo-cutaneous vein; *p. c. a.*, pulmo-cutaneous artery; *pc. v.*, left precaval vein; *pel. v.*, pelvic vein; *ptc. v.*, postcaval vein; *p. v.*, pulmonary vein; *r. a.*, renal artery; *r. at.*, right atrium; *r. p. v.*, renal portal vein; *r. v.*, renal vein; *s. a.*, systemic artery; *sc. a.*, subclavian artery; *ssc. v.*, subscapular vein; *s. v.*, sinus venosus; *t. a.*, truncus arteriosus; *v.*, ventricle.

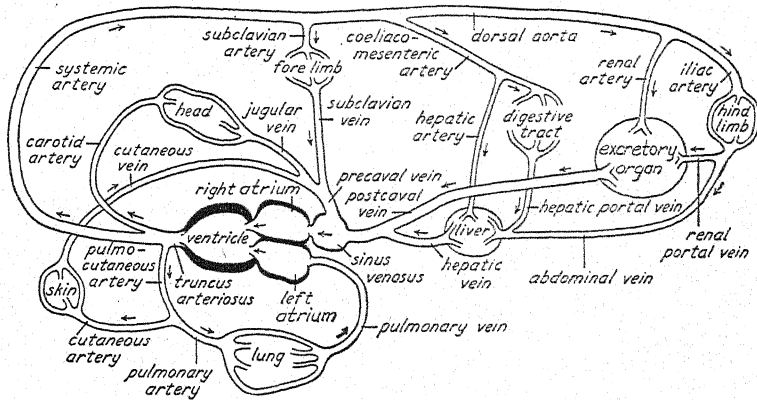


FIG. 21. The circulatory system in a vertebrate having a heart with two atria and one ventricle, as in the frog; diagrammatic. The arrows indicate the direction of circulation.

blood to other parts of the body. The blood from the lungs returns directly to the *left atrium* of the heart; that from other regions is collected in large veins that empty into the *sinus venosus*, which connects with the *right atrium*. When the heart contracts, the two atria contract at the same time and force the blood from both into the single ventricle, which immediately contracts. The opening into the truncus arteriosus is so located that the blood which has come from the right atrium is the first to leave the ventricle. Because of the relatively low resistance in the vessels supplying the lungs, this blood from the right atrium is carried to the lungs. When the pulmonary channels

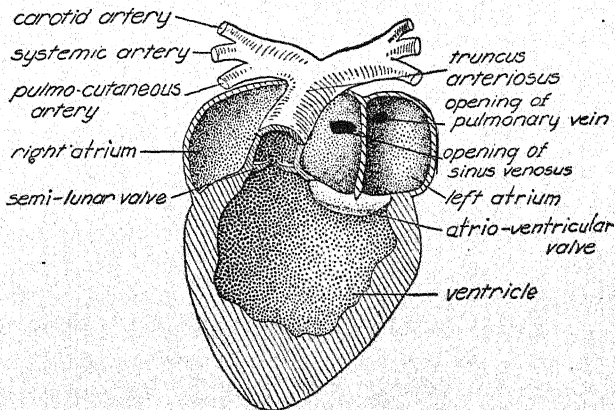


FIG. 22. Heart of the frog, with the ventral walls of the ventricle and atria removed.

are filled, the blood next flows into the systemic arteries. The presence of the so-called *carotid glands* on the carotid arteries makes the resistance very high in those vessels, and they receive the last blood to leave the ventricle, that which came from the left atrium. In this manner, a fairly satisfactory separation of blood from the two atria is made, even though there is but a single ventricle.

In higher vertebrates, such as the birds and mammals, the heart has two ventricles as well as two atria, and two large arteries lead away

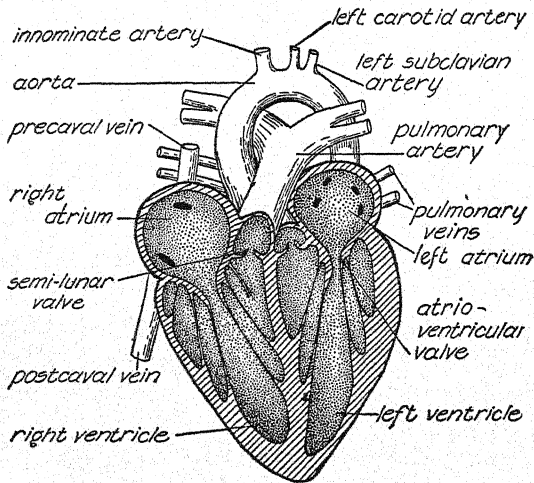


FIG. 23. Heart of man, with the ventral walls of the ventricles and atria removed.

from the heart, one from each ventricle (Fig. 23). The blood distributed by such a four-chambered heart passes through two circuits, one to the lungs and the other to other regions of the body (Fig. 24). There is no problem of separating blood from two sources as in the frog's ventricle. Blood leaves the *right ventricle* through a *pulmonary artery*, which divides to go to the two lungs. After passing through the lung capillaries, the blood returns to the *left atrium* by way of the *pulmonary veins*. From the left atrium the blood passes into the *left ventricle*, which is completely separated from the right ventricle, and flows out into the *aorta*, which divides into vessels leading to the head, trunk, and appendages. From the capillaries in all these regions, blood returns by veins that empty directly into the *right atrium*; the sinus venosus disappears during the evolution of the heart. Blood from the right atrium is emptied into the right ventricle to be sent to the lungs, and so circulation continues.

It has been stated that the usual relation between capillaries and veins is such that blood passes from capillaries into veins, and through them to the heart. Examination of the frog's circulatory system* will show that there are two conspicuous regions where a vein leads from one set of capillaries to another set of capillaries, not to the heart. Thus, blood leaves the capillaries in the walls of the stomach and intestine by way of veins that empty into the *hepatic portal vein*, which passes to a network of capillaries in the liver (Fig. 21). From

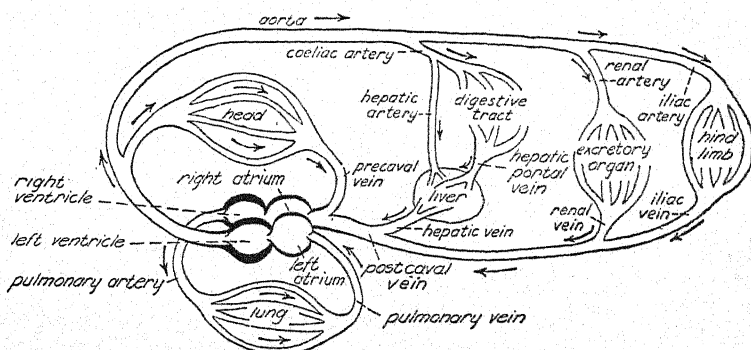


FIG. 24. The circulatory system in a vertebrate having a heart with two atria and two ventricles, as in mammals; diagrammatic. The arrows indicate the direction of circulation.

the liver capillaries, blood drains into the *hepatic vein*, which joins the posterior vena cava, or *postcaval vein*, which empties into the sinus venosus of the heart. This drainage of blood from the capillaries of the digestive tract into the capillaries of the liver is typical of all vertebrates, including man (Fig. 24).

Another pair of *portal veins*, or veins connecting two sets of capillaries, is found in the fishes and amphibians but not in birds or mammals. These are the *renal portal veins*, which receive blood from the capillaries of the hind legs in the frog and carry it to the kidney capillaries (Fig. 21). The capillaries of the kidneys empty into the *renal veins*, which join, from the right and left sides, to form the single postcaval vein that extends to the sinus venosus. When certain changes occurred in the excretory organs during the history of the vertebrate group, the blood vessels of that region were also changed. In mammals, therefore, there are no renal portal veins (Fig. 24). Blood from the capillaries of the hind legs passes into the *iliac veins*, which unite to form the postcaval vein, into which the renal veins empty at the

level of the kidneys. It should be noted here that organs into which portal veins flow also have an arterial blood supply.

This account of the blood-vascular system in vertebrate animals gives the fundamental scheme and the major variations to be found in the group. The idea of a continuous circulation of blood, maintained by the rhythmical contractions of the heart and confined to closed channels, the arteries, capillaries, and veins, must be kept clearly in mind in connection with the discussion of the functions of the circulating fluids.

The Lymphatic System. The lymphatic system is the second part of the circulatory system. Unlike the blood-vascular channels, the lymph vessels do not form a complete system for circulation. The smallest lymph vessels, or *lymphatics*, end blindly among cells and unite to form larger vessels that eventually are connected to the great veins (Fig. 18). In the frog, the *lymph spaces* beneath the skin and the *lymph sinus* dorsal to the kidneys are a part of the lymphatic system, which also includes four so-called *lymph hearts*. In man, there are neither subcutaneous lymph spaces nor lymph hearts, and the lymph vessels connect with only the *subclavian veins* in the anterior part of the thorax. The mammals have many *lymph nodes*, through which the lymph passes on its way to the blood-vascular channels. Lymphocytes (*cf.* p. 98) enter the lymph in these nodes, and large cells called *macrophages* ingest any foreign particles, such as bacteria, which may have gained entrance to the body.

The circulatory system distributes the circulating fluids, the blood and lymph. Blood consists of a fluid, the *plasma*, in which two kinds of cells, the *red* and *white blood cells*, are suspended. When blood enters a capillary network, it is passing under considerable pressure, as a result of the contractions of the heart, into very thin-walled vessels. Under these conditions some of the plasma filters or seeps out through the capillary walls into the slight spaces between the adjacent cells. Also, some of the white cells move out of the blood stream through the walls of the capillaries. Thus, part of the blood leaves the blood vessels and fills the intercellular spaces everywhere in the body. This fluid, outside the blood vessels, is now called *lymph*. Since additions to the supply are continually coming from the blood stream, the lymph slowly passes into the lymphatics and eventually reaches the blood vessels again. The relations between capillaries and lymphatics and between blood and lymph are very important in gaining an understanding of how various substances come to and leave the cells in which the protoplasm is contained (Fig. 18).

The general function of the circulating fluids as what we may call a *common carrier* can be made most clear after a consideration of several other systems. The several phases of this general function are as follows: (1) to carry necessary food materials, including oxygen, to the cells; (2) to carry the waste products of metabolism away from the cells; (3) to transfer hormones, or internal secretions, from one region of the body to another; and (4) in warm-blooded animals, like the mammals, to transfer heat from regions of rapid oxidation and so aid in the maintenance of a constant body temperature. These phases will be referred to as specific illustrations are available in the following sections.

Distribution, Storage, and Assimilation

The fat absorbed into the lymphatics in the submucosa passes, in man, by way of the lymph vessels running in the mesentery to the thoracic duct which empties into the left subclavian vein. The finely emulsified fat is then carried in the blood and, with the amino acids, simple sugars, water, salts, and vitamins, is distributed to all the cells in the body by way of capillary networks. The veins carrying blood from the digestive tract unite to form the hepatic portal vein, which empties into the capillary system of the liver. Here the greater part of the simple sugars absorbed from the intestine leaves the blood and is synthesized in the liver cells to form glycogen, a complex carbohydrate sometimes known as animal starch. As glycogen, carbohydrates are stored in the liver and, to a lesser extent, in the muscles of the body. According to the needs of other cells of the body, glycogen is converted into glucose, passed into the blood stream, and distributed. Interference with the control of the amount of sugar in the blood stream results in abnormal conditions, of which diabetes is the best known. The nature of this control will be discussed in a later section (p. 58). Fat also may be stored in certain regions of the body, such as the deeper regions of the skin (Fig. 25), in the mesentery, in the liver, between the muscles, and, in an animal like the frog, in special organs, the fat-bodies. Like stored carbohydrates, this fat can pass back into the blood for distribution in case of cellular need. So far as we know, amino acids are not stored in any part of the body but are taken from the blood, as required, by all cells.

As a result of the ingestion of food, its digestion, absorption, and distribution, the protoplasm of all the cells of the body receives a supply of the materials that are necessary for its maintenance. The substances brought to the cells are synthesized, under the influence

of cellular enzymes, to form the constituents characteristic of the particular kind of protoplasm in which the synthesis occurs. Thus, finally, we have the assimilation of the foods that enter the body by way of the digestive tract. It has been indicated previously that as-

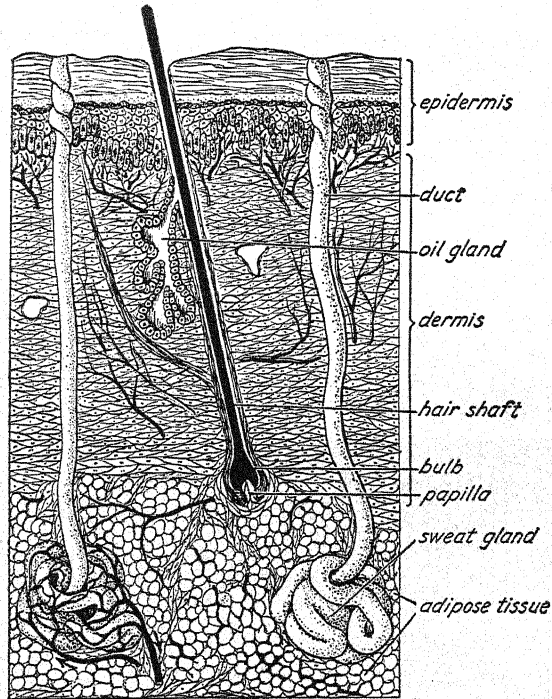


FIG. 25. The skin of man, in section, showing characteristic structures; diagrammatic. The bulb is the so-called root of the hair, where growth occurs. In the papilla, blood vessels and nerves associated with the hair are found. Capillaries are shown around the sweat gland at the left but are dissected away on the right.

simulation is necessary because of the destruction of protoplasmic constituents which must occur if life is to continue. Oxygen is essential for this disintegration of protoplasmic compounds, and we shall now see how it is provided.

The Respiratory System and Respiration

The term respiration has been widely used to cover the so-called gaseous metabolism of an organism. It seems unnecessary to try to separate the metabolism of oxygen from that of other substances,

since all metabolic reactions are so closely interrelated. If food is to be defined as any substance necessary for the normal functioning of the organism, oxygen is a food, just as water and mineral salts are foods. *Respiration*, then, as used here can be defined as the process by which oxygen is supplied to the protoplasmic system. This process has two phases, known as external respiration and internal respiration. It is with the first that the respiratory system is concerned.

Respiratory Organs. Respiratory organs are of two kinds: *gills* in water-dwelling vertebrates and *lungs* in land dwellers. Gills occur along the sides of the pharyngeal pouches in fishes and some amphibians and are covered by a very thin layer of cells. Beneath this covering layer is a rich capillary net. In vertebrates with lungs, there are always air passages, which are also a part of the respiratory system.

The frog has a primitive respiratory system. The lungs are simple sacs with the inner surfaces somewhat folded. They are located in the anterior part of the pleuro-peritoneal cavity and are connected directly with a chamber, known as the *larynx*, which contains the vocal cords (Fig. 1). The larynx has a slitlike opening, the *glottis*, into the pharynx. The nasal canals lead into the mouth cavity. In breathing, the frog must keep its mouth closed, since the volume of the mouth cavity and pharynx is changed by the lowering and lifting of the floor of the mouth cavity. When the floor of the mouth cavity is lowered, air is pulled in through the nostrils and nasal canals, which can then be closed. When the floor of the mouth cavity is lifted and the glottis opened, air is pushed into the larynx and into the cavities of the lungs. Air is expelled from the lungs by contractions of the body wall when the nostrils are open.

In man the respiratory system is more complex, and the method of breathing entirely different. Again, there is a glottis opening from the pharynx into a larynx, where the vocal cords are located (Fig. 14). However, a rather long tube, the *trachea*, leads from the larynx into the thorax, where division into two bronchi occurs. The *bronchi* extend into the lungs, which are made up of small air chambers, each directly continuous with a minute subdivision of a bronchus. The air cavities of the human lung can be roughly likened to a bunch of grapes; the branching stem would represent the bronchi and bronchioles, and the grapes the air chambers. Each lung lies in a closed *pleural cavity* which is separated from the abdominal cavity by the *diaphragm*, a muscular partition, and surrounded by the ribs, spinal column, and sternum, or breastbone (Fig. 5). Breathing is the result of increasing and decreasing the volume of the pleural cavities by movements of the diaphragm and ribs. When the capacity of the closed pleural cavities

is increased by lowering the diaphragm and lifting the ribs, air rushes into the lungs through the air passages. A reduction in the volume of the pleural cavities forces air out of the lungs.

Respiration. In both the frog and man, there is a rich supply of capillaries beneath the layer of cells lining the cavities of the lungs. The inner surface of the lining layer is always moist, just as is the surface of the gills or of the skin in a frog. Under such conditions, oxygen will pass through the cellular layer into the blood in the capillaries beneath, since the circulating blood will contain less oxygen than the water or air. This passage of oxygen into the blood is known as *external respiration*; typically it follows inhalation, or the filling of the lungs with air. It is very unusual for a land-dwelling animal to carry on external respiration through its skin as the frog does.

External respiration is analogous to the absorption of nutrients from the digestive tract. However, the passage of oxygen from the lung to the blood is explained adequately in terms of diffusion from a region of high concentration to one of lower concentration. The concentration of oxygen in the water or air is greater than that in the blood, from which the oxygen is constantly removed by the cells of the body; oxygen diffuses in the direction of the blood to establish an equilibrium. In the blood stream the oxygen enters into a loose combination with *hemoglobin*, an iron compound carried by the red blood cells, and is distributed throughout the body in that way. This combination with hemoglobin, which is known as oxyhemoglobin and is responsible for the red color of oxygenated blood, is unstable, and in the regions of the capillary networks free oxygen leaves the blood by diffusion and passes into the cells. This passage of oxygen into the protoplasmic system is designated *internal respiration* and immediately precedes the reactions of dissimilation.

Dissimilation. Dissimilative metabolic activities include those reactions by which protoplasmic constituents are chemically decomposed with the transformation of energy. The reactions that transform energy with the inevitable production of heat are *oxidations*, that is, reactions in which oxygen unites with compounds of the protoplasmic system. Oxidation is commonly known as combustion, or burning. When fuel burns, oxygen from the air is combined with the chemical compounds that make up the fuel, liberating energy which can be made to do work and producing heat. It was Lavoisier, in 1777, who first recognized the similarity between the combustion of fuels and oxidation as it occurs in the bodies of animals. The statement is sometimes made that "food" is oxidized in our bodies to liberate energy with the production of heat. It is well to keep in mind that

this is true only in the sense that organic foods, broken down into their simple structural units, are assimilated by the protoplasm of cells. The protoplasmic constituents, synthesized from nutrients delivered to the cells, are the compounds that undergo dissimilation. Oxidation of carbohydrates and lipids goes to completion in the body, and the combustion of these classes of compounds is the chief source of energy in animals. Proteins are also oxidized to some extent, but the incompleteness of the reaction makes it impossible to regard them as primary sources of energy. Dissimilation results in the formation of chemical by-products of such a nature that they are no longer of use in the protoplasmic system. The combination of oxygen with carbohydrates and lipids gives rise to carbon dioxide and water; with proteins the end products are carbon dioxide, water, and a variety of nitrogen-containing compounds. These materials are the waste products of metabolism and are known as *excretions*.

Excretion and the Excretory Organs

Excretion. Excretions must be constantly removed from the cells in order that the normal oxidation reactions may continue. It is well known that, if ashes are permitted to accumulate, a fire will be put out by these waste products of its burning. The continuity of a chemical reaction depends likewise upon the removal of its end products. The process of removal of the waste products of metabolism is called *excretion*, and the places of removal are chiefly the lungs, skin, kidneys, and liver. The excretions are carried from all the cells of the body in the blood stream. In land-dwelling vertebrates, as blood passes through the lung capillaries, the carbon dioxide diffuses into the cavities of the lungs and is exhaled. In aquatic forms this waste gas is eliminated into the water surrounding the gills. The excretion of carbon dioxide is sometimes included under the heading of respiration. Carbon dioxide is, however, one of the metabolic wastes, and its discharge is included under the heading descriptive of the removal of water and nitrogenous excretions. Exhaled air is moist, because the lungs also excrete water. From the skin of man, carbon dioxide, water, certain salts, and minor quantities of nitrogenous substances are excreted as perspiration. In the frog the amount of carbon dioxide excreted by the skin is relatively large, and the loss of water is considerable. About 50 per cent of the water, traces of carbon dioxide, and the nitrogenous wastes, in the form of *urea*, are discharged as *urine* through the ducts of the kidneys. Urea is not produced, as

such, in the cells throughout the body or in the kidney. It is built up from ammonia in the liver, from which it is carried to the kidneys.

In addition to the typical excretory products produced by dissimulation in all cells of the body, there are other substances which must be eliminated if the organism is to remain normal. One of these is the pigment bilirubin, formed by the disintegration of hemoglobin when red blood cells die and are destroyed. Bilirubin is excreted by way of the liver and is the pigment chiefly responsible for the color of the bile. Jaundice results if for any reason this excretion does not occur. The liver also excretes cholesterol, which arises, at least in part, from the destruction of red blood cells. Certain types of gallstones are almost pure cholesterol, which is one of the derived lipids. Various drugs, certain poisons, and metals such as copper and iron, none of which are excretions as we have defined them, are eliminated from the body in the bile secreted by the liver. These substances are dissolved in the bile and are carried to the large intestine, where they are found in the feces and eliminated when egestion occurs.

Excretory Organs. The lungs, the skin, the liver, and the excretory organs are, therefore, organs in which excretion occurs, but they do not make up a system of organs in the ordinary meaning of the term. In dividing the body into systems it is convenient to assign a particular function to a single group of organs, a system. For that reason the lungs are discussed as a part of the respiratory system, the skin as a part of the integumentary system, which functions as a covering for the body, and the liver as a part of the digestive system. In the skin of a number of animals, including man, there are sweat glands from which watery solutions pass to the outer surface of the body by way of ducts (Fig. 25). This is one way of eliminating waste products of metabolism. The excretory organs and their ducts are, however, referred to as the *excretory* or *urinary system*. Since the ducts of the excretory organs are also used for the discharge of male reproductive cells in vertebrates like the fishes and amphibians, the excretory and reproductive organs are frequently referred to as the *urino-genital system* (cf. Fig. 67, p. 122). In this account we shall not be concerned with this dual system but shall describe the structure of the urinary system.

Two different kinds of functional excretory organs distinguished by the method of their origin during development are found in adult vertebrates. The first of these, the *mesonephros*, is present in adult fishes and amphibians and appears and disappears during the development of reptiles, birds, and mammals, in which a *metanephros* is formed as the excretory organ of the adult. Although both mesonephroi

and metanephroi are often called the *kidneys*, this term should be reserved for the metanephroi. The excretory organs are paired structures located on the dorsal wall of the coelom and not suspended in it (Fig. 2). Tubes or ducts, called the *excretory ducts*, extend from the excretory organs of the frog to the dorsal surface of the cloaca. A *urinary bladder*, or reservoir where urine is stored before it is voided,

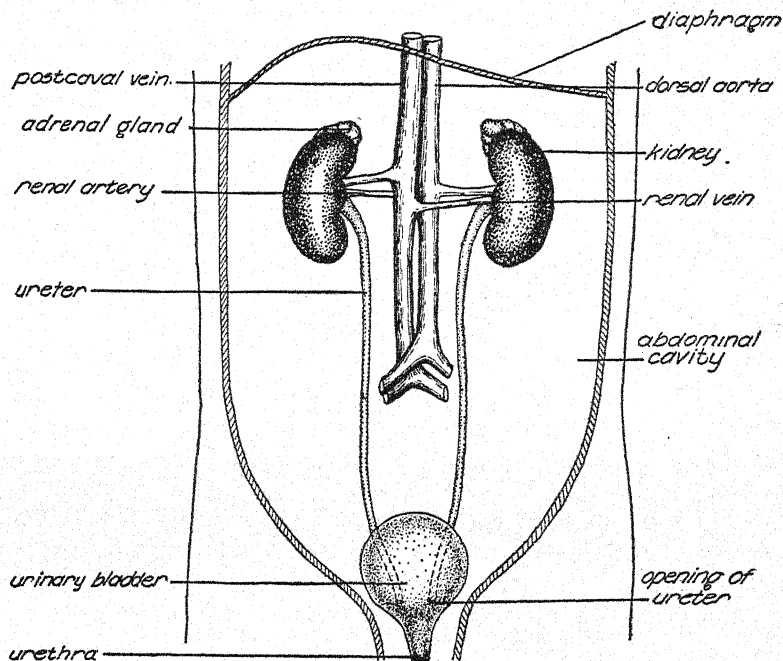


FIG. 26. Excretory system and related structures of man.

is connected to the ventral surface of the cloaca opposite the openings of the excretory ducts (Fig. 1). In mammals, the excretory ducts are known as *ureters* and discharge the urine directly into the bladder, from which it is emptied to the outside without passing through the posterior part of the digestive tract (Fig. 26). If the structure of the excretory organ is examined carefully, numerous small tubes, the *excretory tubules*, are found to open at one end into the excretory duct. The other end of an excretory tubule ends in a cup known as *Bowman's capsule*, which contains capillaries that arise from branches of the renal artery (Fig. 27). Each of these groups of capillaries is a *glomerulus*, which with its surrounding Bowman's capsule makes up a *renal corpuscle*. The excretory tubules are surrounded by a very conspicuous capillary network. In the frog these capillaries are fed by

the renal portal vein as well as by the renal arteries, but there is no renal portal vein in man.

Blood in the thin-walled capillaries of the glomerulus is under considerable pressure because the vessel leading away from the capillary bed is smaller than the one discharging blood into it. As a result, all constituents of the blood except its cells and plasma proteins are filtered through the walls of Bowman's capsule into the lumen of the excretory

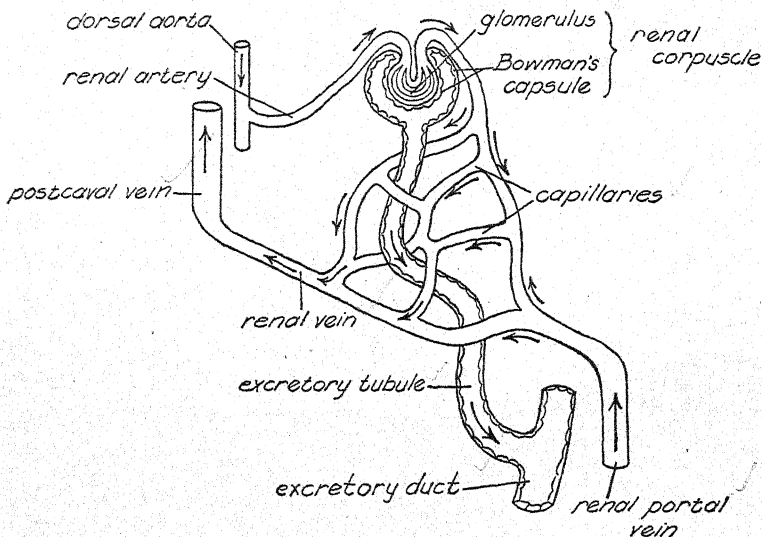


FIG. 27. An excretory tubule and blood vessels in the excretory organ of the frog; diagrammatic (cf. Fig. 67, p. 122).

tubule. The composition of this fluid is changed as it passes toward the excretory duct. Substances needed by the body, such as glucose, chlorides, bicarbonates, and phosphates, are absorbed by the cells of the tubules, and the fluid is concentrated by the absorption of water. Under certain circumstances substances are added to the fluid by the cells lining the tubules, but it has not been established that this is a normal process in kidney tubules like those described here. The fluid as it reaches the excretory duct is known as *urine*.

Summary

In this chapter we have considered the systems of organs that have functions relating to the capacity of metabolism, which is one of the characteristics of living organisms. When great numbers of cells exist together as they do in complex multicellular animals like the verte-

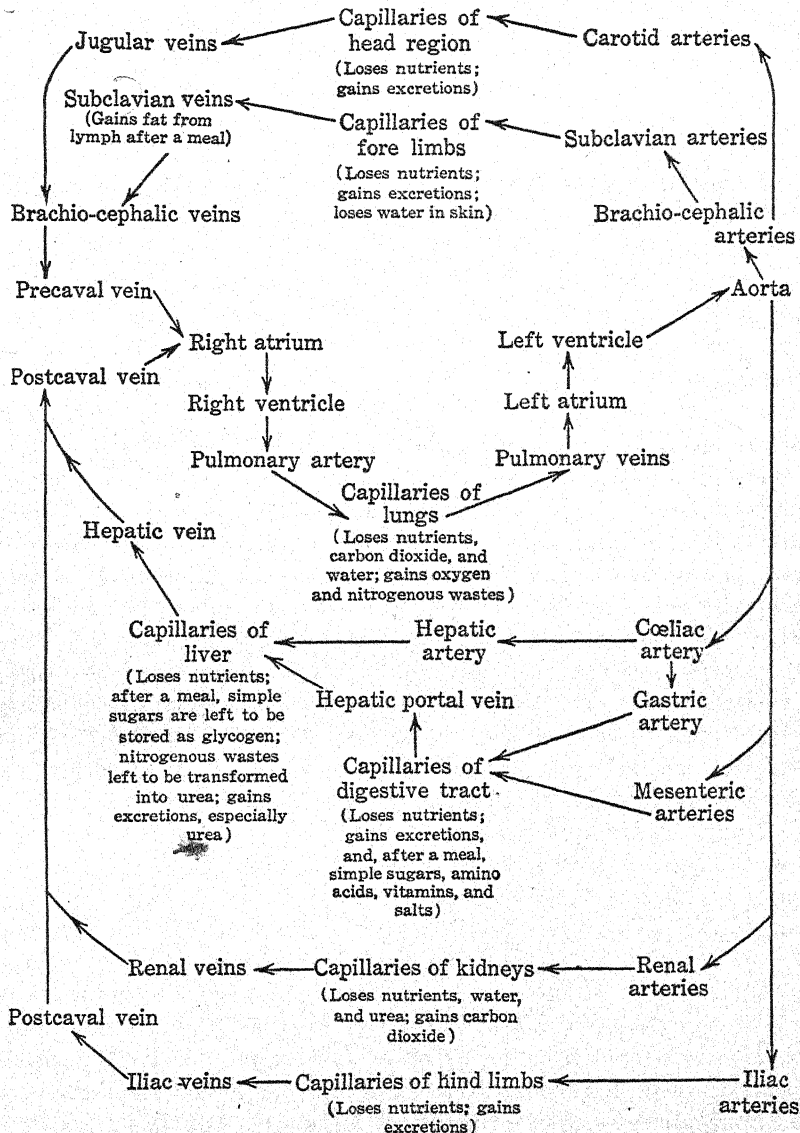


FIG. 28. Word-diagram showing the principal blood vessels in man, the path of the blood to various regions of the body, and the chief losses and gains of the blood. The term nutrients includes simple sugars, amino acids, fats, vitamins, salts, and oxygen; the term excretions includes carbon dioxide, water, and nitrogenous compounds.

brates, it is impossible for each cell to obtain its food materials and to discharge its excretions independently. It is apparent that the only way so many cells can live together is by being mutually dependent. The cells of all multicellular organisms show some degree of interdependence, and in the larger ones are organized into organs and systems which function in such a way that the individual cells are able to carry on the metabolic reactions that are responsible for the animal's life. The digestive system serves to prepare nutrients, other than oxygen, so that they can be absorbed and assimilated; respiratory organs deliver oxygen to the blood; and excretory organs are the places of discharge for the waste products of metabolic reactions. The individual cells of the body are surrounded by lymph, which is derived from the blood, and by means of these two circulating fluids, materials are transported to and from all cells (Fig. 28). When the simple sugars, amino acids, vitamins, water, and mineral salts are absorbed from the small intestine, they pass into the plasma of the blood. The lipids, absorbed into the lymph, are soon discharged by way of the great veins into the blood plasma for distribution. Oxygen, obtained from the environment, reaches the blood by the process of external respiration and enters into combination with the hemoglobin of the red blood cells. The materials which are necessary for maintenance of the chemical reactions of the protoplasm are carried into capillary networks all over the body and pass from the blood into the lymph surrounding the cells and so into the cells where they are used (Fig. 18). Carbohydrates and fats may be left in large amounts at storage depots, to be picked up later for distribution. Carbon dioxide, water, and nitrogenous wastes, resulting from dissimilation within the cells, pass out into the lymph around the cells and so into the capillaries. These waste products are carried in the blood to the places of excretion. The exchange of foods and excretions between the blood and the cells by way of the lymph can apparently be explained adequately on the basis of diffusion from regions of higher to those of lower concentration.

If the physiology of metabolism in vertebrate animals is considered and mastered from the point of view of the chemical reactions occurring in its individual cells, the study of function in other types of animals will be merely a reaffirmation of the facts brought out in this chapter. The general protoplasmic requirements and reactions are assumed to be the same throughout the Animal Kingdom. Another important fact to keep in mind is that, although the cell is the unit of function, the reactions of the animal as a whole depend upon the coördinated activities of all its cells, which make possible what we shall call the physiological balance of the organism.

CHAPTER 3

VERTEBRATE ORGAN-SYSTEMS RELATED TO IRRITABILITY

The organ-systems related to metabolism perform certain functions which are necessary if the protoplasm in individual cells is to remain alive. In order for the animal as a whole to exhibit the typical reactions of a living organism—to behave as an individual—its many systems must be coördinated, or must work together. If any system ceases to function, an organism cannot remain alive, and it becomes abnormal if the activities of its organs are not correlated in the usual way.

Coördination is possible because protoplasm has the capacity of *irritability*; it responds by internal reaction to a stimulus, or change in its environment. A change in the surroundings of a cell is followed by a reaction of the cell. There are two ways of altering the environment of cells in the vertebrate body. One is by means of substances that circulate in the blood, and the other is by means of impulses that pass along the nerves, which penetrate to every part of the animal. As the result of secretions which enter the blood from the endocrine or ductless glands, what is known as *chemical coördination* is possible. *Nervous coördination* occurs as a result of the activities of the sense organs and nervous system.

Endocrine Glands and Chemical Coördination

Reference has been made to glands, or organs of secretion, which possess ducts and pass their secretions on to body surfaces (*cf.* p. 29). There are a number of glands which do not have ducts by which to discharge their secretions but which pass them into the blood stream. Such glands are known as the *ductless glands*, *glands of internal secretion*, or *endocrine glands*. Their secretions are called *internal secretions*, *endocrines*, or *hormones*. A well-known example of chemical coördination which follows the distribution of hormones by the blood is the control of the flow of pancreatic juice. This fluid is not passed into the small intestine continually but only when food is present. It

was supposed for a long time that the release of pancreatic juice was conditioned by nervous coördination. Experiments demonstrated that the nerves leading to the pancreas can be cut without affecting the control of the flow of pancreatic juice. It was then discovered by Bayliss and Starling in 1902 that, if the blood vessels are tied so that blood does not enter the capillaries of the pancreas, the pancreatic juice is not discharged when food enters the intestine. Further study revealed that, when the contents of the stomach enter the small intestine, the hydrochloric acid stimulates certain cells in the intestinal mucosa to discharge into the blood an endocrine substance known as *secretin*. The secretin, reaching the pancreas by way of the blood, stimulates the pancreatic cells to secrete pancreatic juice, which then passes to the small intestine by way of the pancreatic duct.

Endocrinology, or the study of the effects of endocrines or hormones, is a relatively new field of investigation, and information concerning many of its phases is incomplete. The glands of the endocrine system are very closely interrelated, and normal function is secured when all are acting in a state of balance. Certain effects are, however, particularly referable to individual glands. The nature of the functions of the endocrine glands can be determined by observing individuals who have diseased glands or from whom a particular gland has been removed, by transplanting glands from one individual to another, and by feeding dried glands or injecting extracts of the glands. The best-known endocrine glands are the thyroid, parathyroids, adrenals, pancreas, hypophysis or pituitary, and the reproductive organs. In addition, there are more or less isolated endocrine-secreting cells, such as those that produce secretin. It is possible that organs other than those named may have endocrine function.

The *thyroid gland* in man is located on the sides of the trachea posterior to the larynx (Fig. 29, cf. Fig. 4, p. 11). *Thyroxin*, which is the active principle of the secretion of the thyroid gland, was isolated in 1916 and synthesized in 1927. It has a pronounced effect on the rate of metabolism, since it regulates the rate of cellular oxidations, or dissimilation. Too much thyroxin increases the rate of oxidation so that the organism tends to burn itself up faster than it can rebuild its protoplasm. Thyroxin contains iodine, which is the important part of the molecule in so far as its effect on the metabolic rate is concerned. *Endemic goiter*, which is common in certain regions in which there is little iodine in the soil and drinking water, is an enlargement of the thyroid gland resulting from a copious secretion which is apparently an attempt to compensate for the lack of iodine. Iodides, regularly added to the diet, will relieve this condition. In children extreme defi-

ciency of thyroid secretion, or hypothyroidism, results in the disease known as *cretinism*, in which neither physical nor mental development is normal. Cretinism can be remedied by administration of thyroxin if this treatment is started before the individual is too old. In adults sub-normal thyroid secretion produces a condition known as *myxædema*, strikingly characterized by swollen, dry skin and resulting in mental impairment. Here, again, administration of extracts is helpful in some cases. On the other hand, hyperthyroidism, or oversecretion by

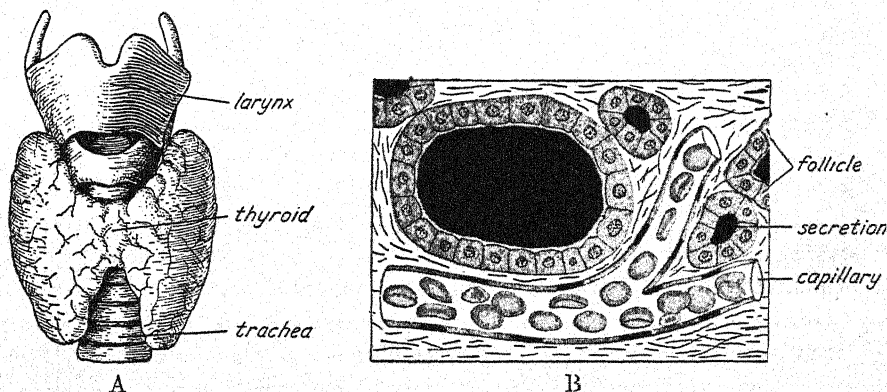


FIG. 29. The thyroid gland. A, the gland of man as seen from the front, showing its position with reference to the larynx and trachea. B, diagram of a section of the gland, showing the follicle cells which produce the secretion and the capillaries by way of which it is distributed.

the thyroid gland, may occur. In extreme cases this results in *exophthalmic goiter*, characterized by an enlarged thyroid gland, rapid pulse, moist skin, protruding eyeballs, and nervous symptoms of excitability and restlessness. This condition may be remedied by removal of a part of the gland so that the amount of secretion is reduced to normal.

The *parathyroids*, of which there are two pairs in man, are very small and are embedded in the thyroid gland. The active principle of the parathyroids was isolated in 1925 but has not been chemically identified; it regulates the concentration of calcium in the blood. Too little of the parathyroid secretion results in a decrease in the calcium content of the blood. Pronounced deficiency produces *parathyroid tetany*, in which an individual may die in convulsions. Administration of parathyroid extract will relieve this condition. If the parathyroids produce too much secretion, a condition of hyperparathyroidism occurs; the calcium content of the blood is very high, and calcium may be withdrawn from the bones.

The *adrenal glands*, or *suprarenal glands*, which in the frog lie on the ventral surface of the kidneys and in higher vertebrates come to lie anterior to the kidneys, are composed of two regions, a central medulla and a surrounding cortex (Fig. 26, p. 51). Each of these regions is a gland of internal secretion. The active principle of the secretion of the medulla is known as *adrenalin*, or *epinephrine*, and was isolated in 1901. Adrenalin was first synthesized in 1904. It is widely used as a drug in the control of hemorrhage and asthma, but it has not been established that the secretion of the medulla has any effect on the walls of blood vessels in the normal animal. When the amount of adrenalin in the blood stream is increased, the transformation of glycogen into sugar, which passes into the blood, is hastened. Adrenalin secreted by the medulla of the adrenal gland is identical with the secretion produced by a certain type of nerve ending (*cf.* p. 86). Extracts of the cortex of the adrenal glands have yielded a large number of crystalline compounds. Some of these, for example, *desoxycorticosterone*, maintain a normal water and salt balance in animals from which the adrenals have been removed. Others, for example, *corticosterone*, affect carbohydrate and protein metabolism. A fraction of the extract from which a crystalline substance has not been obtained still has life-maintaining qualities. Which, if any, of the numerous substances obtained from the adrenal cortex is the secretion it normally passes into the blood stream remains for future research to determine. An animal from which the cortex of the adrenal glands has been removed dies unless cortical products are administered. *Addison's disease* in man, long known to be the result of insufficient secretion by the adrenal cortex, can now be controlled by treatment with cortical products.

The *pancreas* is composed of two kinds of secreting cells. The pancreatic juice, which has already been mentioned, is passed into the small intestine by way of the pancreatic duct and is important in digestion. In addition to the cells elaborating this secretion, the pancreas contains groups of cells known as the *islands of Langerhans*, which secrete a hormone that is discharged into the blood (Fig. 30). The active principle of this secretion was named *insulin* and isolated in 1922. It was prepared in crystalline form in 1927. If this secretion is absent, sugar is present in excessive amounts in the blood and is excreted in the urine. This is a major symptom of the disease known as *diabetes*. Injections of insulin are effective in controlling diabetic symptoms. Its isolation and the technique of its use constitute important medical achievements.

From the brief accounts of some of the endocrine glands the student must not get the impression that each one acts alone. In cases of imbalance a number of these glands seem to be involved. The endocrine disturbances that have been cited in this account are the results of serious divergences from the normal coördination.

The relations between endocrine glands in the normal coördination of mammals may be illustrated by the interaction between the *hypo-*

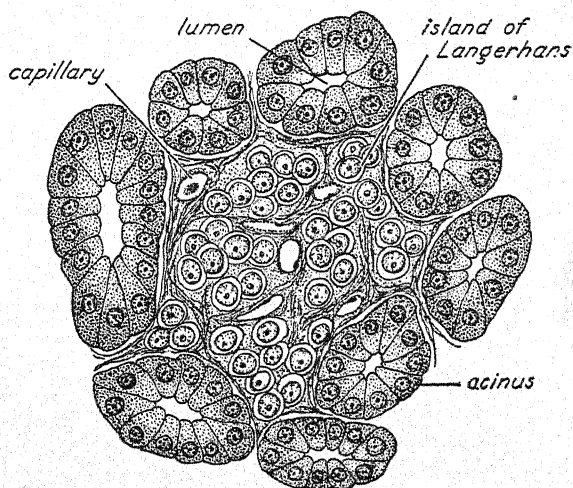


FIG. 30. The pancreas, showing an island of Langerhans, the cells of which produce the hormone of the pancreas, surrounded by acini, the cells of which secrete the pancreatic juice; seen in section.

physis, or *pituitary gland*, and the reproductive organs¹ in the control of the reproductive cycle. The hypophysis, located ventral to the brain, is composed of an anterior and a posterior lobe, both of which secrete hormones (cf. Fig. 14, p. 27, and Figs. 32 and 33). The secretion of the anterior lobe conditions a number of interesting effects. In young animals it is a regulator of growth, which can be noted easily in the long bones. Oversecretion during youth results in *gigantism*, and *acromegaly*, or unusual growth of the bones of the hands, feet, and face, occurs under similar conditions in adults. Inadequate secretion occurs in certain dwarfs. Another effect of the secretion of the anterior lobe, in which several active principles have been postulated but none chemically identified, is upon the reproductive organs in sexually ma-

¹ See Chapter 5, pp. 121-129, for an account of the reproductive system and its function in vertebrates.

ture mammals. In males neither the production of spermatozoa nor the differentiation of the interstitial cells of the testes occurs in the absence of the anterior lobe of the hypophysis. Similarly, in females it can be demonstrated that growth and differentiation of egg cells and their surrounding follicles are conditioned by the secretion of the anterior lobe. If the interstitial cells of the testis become differentiated, they produce a hormone which conditions the differentiation of the accessory glands of the male reproductive tract, the normal appearance of the so-called secondary sex characters, such as growth of hair and the general body proportions, and the mating tendency. The active agent in this hormone is called *testosterone*; it was crystallized and synthesized in 1935. As the follicles grow in the ovary, they give rise to a secretion which has a stimulating effect upon the differentiation of the cells in the wall of the uterus and, in mammals other than the primates, conditions the willingness to mate. This hormone contains what are known as *estrogenic substances*, a number of which have been isolated in crystalline form since 1929. Estrogenic substances have also been synthesized. When the egg cell is mature, its follicle ruptures, and the egg is freed into the reproductive tract. Then the old follicle undergoes further differentiation and becomes a corpus luteum, which gives rise to a new kind of secretion. The active principle of this is called *progesterone*; it was crystallized in 1934 and prepared artificially for the first time in the same year. Under the influence of this substance the lining of the uterus is finally prepared to receive and provide nourishment for the development of a fertilized egg, and pregnancy is maintained.

The endocrine control of the reproductive cycle as outlined in the last paragraph illustrates the nature of chemical coördination. It should be noted that, although hormones circulate in the blood and are present in the environment of all cells, only certain cells respond to a particular hormone and often they are not continuously sensitive. In some cases it is known that the amount of the hormone in the blood varies in a regular way; that is, the rate of secretion by the endocrine gland may not be uniform. A certain concentration must be present before a stimulus results. In other cases it appears that cells of the organ typically responding to a particular internal secretion do so only at definite stages in their differentiation; that is, the cells are not equally stimulable at all times. Under normal conditions the interrelations between level of hormone production and sensitivity of effector cells are so nicely balanced that the activities of different organs are adequately coördinated.

Systems and Organs Related to Nervous Coördination

The nervous system of vertebrates is the system primarily responsible for nervous coördination. However, the nervous system is so intimately related to the sense organs and to the muscles that we some-

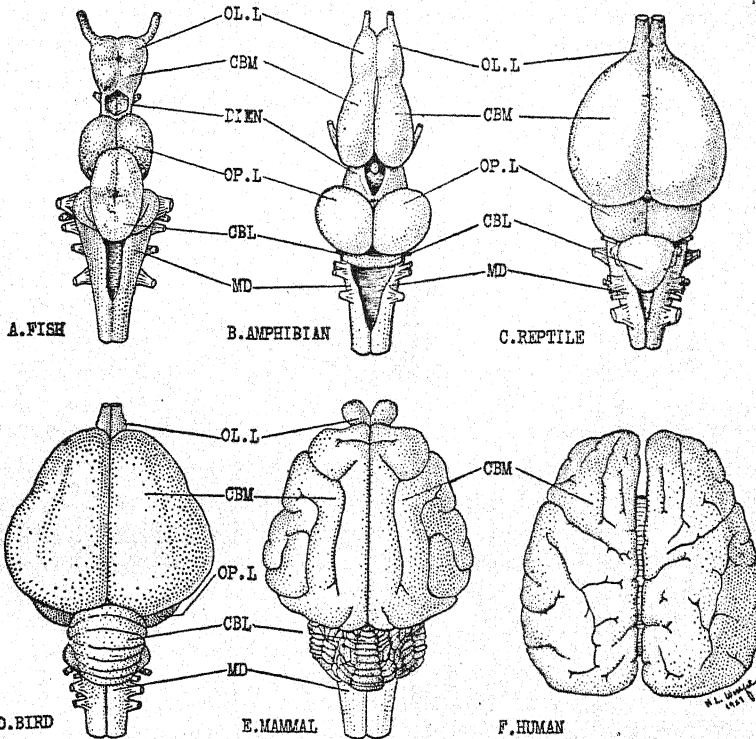


FIG. 31. Brains of representative vertebrates, from dorsal view (cf. the lateral views shown in Fig. 494, p. 680). *CBL*, cerebellum; *CBM*, cerebral hemispheres; *DIEN*, diencephalon; *MD*, medulla oblongata; *OL. L.*, olfactory lobe; *OP. L.*, optic lobe.

times speak of a sensory-neuro-muscular system. The skeletal system is entirely unrelated to the function of the nervous system but serves for its protection. Since, in addition, the function of locomotion is dependent on the attachment of muscles to hinged bones, the skeleton will be considered briefly in this section.

The Nervous System. The nervous system of vertebrates is divided for purposes of discussion into two parts: the central nervous system and the peripheral nervous system. The *central nervous sys-*

tem is composed of the brain and spinal cord. The *peripheral nervous system* consists of the nerves which connect the brain and spinal cord with all parts of the body.

The Central Nervous System. The central nervous system develops in the same way in all vertebrates. Soon after its first appearance it is found to have five regions in the brain, which can be distinguished from the spinal cord. These five regions are known, from anterior to posterior, as the telencephalon, diencephalon, mesencepha-

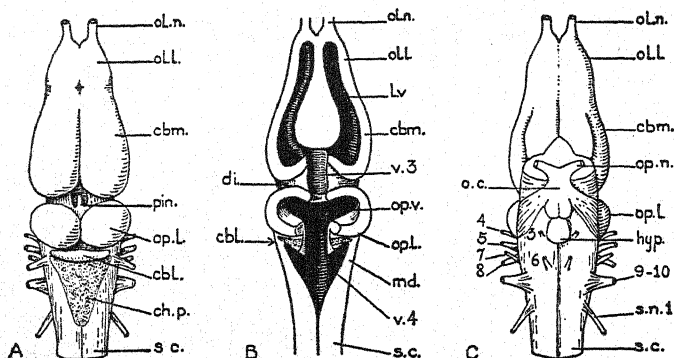


FIG. 32. Brain of the frog. *A*, from dorsal view. *B*, in horizontal section to show ventricles. *C*, from ventral view. *cbl.*, cerebellum; *cbm.*, cerebral hemisphere; *ch. p.*, choroid plexus of 4th ventricle; *di.*, diencephalon; *l. v.*, lateral ventricle; *md.*, medulla oblongata; *o. c.*, optic chiasma; *ol. l.*, olfactory lobe; *ol. n.*, olfactory nerve; *op. l.*, optic lobe; *op. n.*, optic nerve; *op. v.*, optic ventricle; *pin.*, pineal gland; *hyp.*, hypophysis or pituitary gland; *s. c.*, spinal cord; *s. n. 1*, 1st spinal nerve; *v. 3*, third ventricle; *v. 4*, fourth ventricle; *3, 4, 5, 6, 7, 8, 9, and 10*, cranial nerves.

lon, metencephalon, and myelencephalon, constituting the "brain stem" (*cf.* Fig. 89, p. 148). None of these parts is lost in any vertebrate, but differences in the degree of development of certain regions, especially the telencephalon and the metencephalon, characterize different classes of vertebrates. The cerebral hemispheres develop from the dorsal part of the telencephalon, and the cerebellum arises from the dorsal part of the metencephalon. Figure 31 and Fig. 494, p. 680, show the relative development of cerebral hemispheres and cerebellum in different vertebrates. It will be noticed that the brain of man seems to be composed of only cerebral hemispheres, because they have overgrown the other parts of the brain (*cf.* Fig. 14, p. 27).

When the brain of the frog is examined from the dorsal view, five main parts, derived from the five primitive brain vesicles, can be seen (Fig. 32 *A*). The most anterior region consists of the paired *cerebral*

hemispheres, from which the *olfactory lobes* are incompletely separated. Posterior to the cerebral hemispheres is a narrowed region, the *diencephalon*, from the dorsal surface of which arises a rudimentary structure, the *pineal body*, which is of interest because it is developed as a simple eye lying in the dorsal midline in some of the reptiles. The *optic lobes* are a pair of conspicuous rounded bodies behind the diencephalon. Posterior to them is a narrow transverse ridge, the *cerebellum*, followed by the *medulla oblongata*, which is continuous with the spinal cord.

When the brain is viewed from the ventral surface, the *optic chiasma*, or the region where the optic nerves cross one another, and the *hypophysis*, ventral to the diencephalon, can be observed (Figs. 32 C and 33). As on the dorsal surface, the most posterior region is the *medulla oblongata*. The medulla is continuous posteriorly with the *spinal cord*, which ends in a very slender terminal region known as the *filum terminale* (Fig. 33).

One of the distinguishing characteristics of the Phylum Chordata is the presence of a dorsal, tubular, central nervous system. The brain and spinal cord of vertebrates contain a continuous cavity, which is expanded to form the *ventricles* of certain regions of the brain and reduced to the microscopic *central canal* in the spinal cord (Fig. 32 B). The *anterior* and *posterior choroid plexuses* are composed of the thin roofs of the diencephalon and medulla oblongata, respectively, together with the highly vascularized *pia mater*, or innermost of the membranes surrounding the brain (Fig. 32 A). These rich vascular beds are carried into the cavities of the third and fourth ventricles by the down-growth of the thin-walled regions. An extension of the anterior plexus passes into the ventricle of each cerebral hemisphere. The cavity of the central nervous system is filled with the *cerebro-spinal fluid*, which is chiefly filtered from the blood stream in the plexuses. This fluid also surrounds the brain and spinal cord and has a cushioning, protective function. A slow circulation is maintained, since the cerebro-spinal fluid returns to the blood stream by way of the venous channels in the outermost of the brain membranes, the *dura mater*.

The Peripheral Nervous System. The peripheral nervous system is composed of the cranial, spinal, and autonomic nerves. In the frog there are ten pairs of *cranial nerves* which are continuous with the brain (Figs. 32 and 33). All of them pass to the head and neck with the single exception of the tenth pair, or *vagus nerves*, which have branches running to the lungs, heart, and digestive tract. These ten pairs of cranial nerves occur with slight modifications in all vertebrates. In addition, an eleventh and twelfth pair of cranial nerves

are found in reptiles, birds, and mammals. The *spinal nerves* of vertebrates are continuous with the spinal cord and vary in number

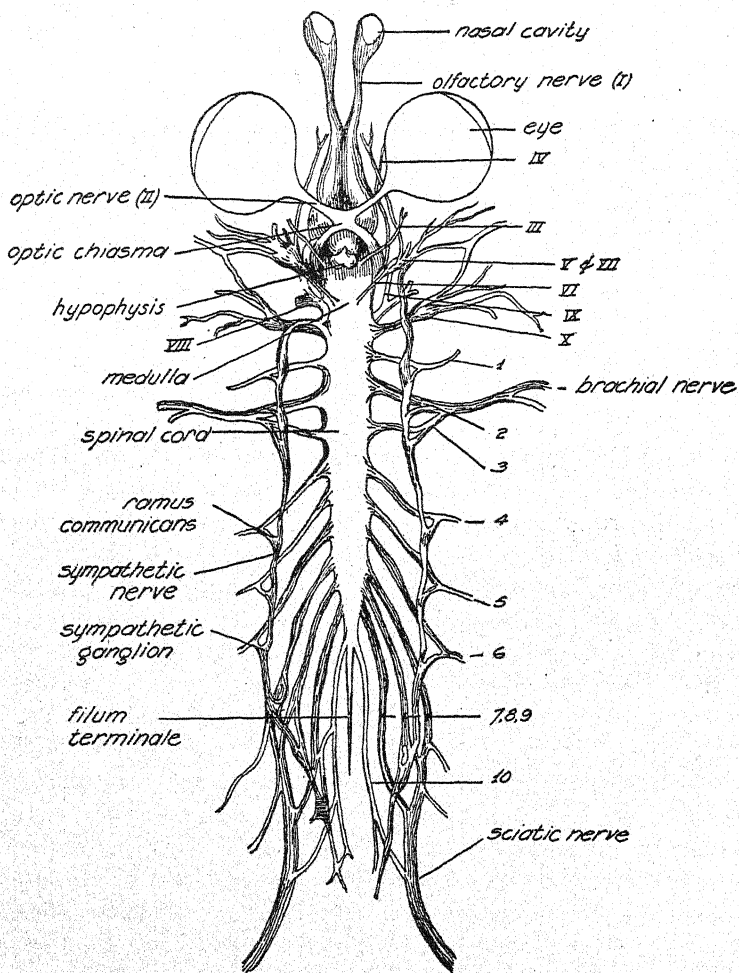


Fig. 33. Nervous system of the frog, from ventral view. I-X, cranial nerves; 1-10, spinal nerves.

(Redrawn from R. Wiedersheim, "Comparative anatomy of vertebrates," copyright, 1907, by The Macmillan Co., printed by permission.)

according to the number of segments in the vertebral column. In the frog there are nine well-developed spinal nerves and a smaller tenth nerve (Fig. 33); in man, there are some thirty pairs of spinal nerves, if the rudimentary nerves at the posterior end of the cord are counted. The spinal nerves extend to the muscles and skin of the trunk and

limbs. The *autonomic nerves* are not directly continuous with the central nervous system but are made up in part of fibers that extend to the brain or spinal cord by way of some of the cranial and spinal nerves. Autonomic nerves are characterized by the presence of ganglia at some distance from the central nervous system. Any impulse leaving the central nervous system over a fiber which becomes part of an autonomic nerve is relayed in one of these ganglia to a second nerve fiber over which it reaches the effector, where discharge occurs. The

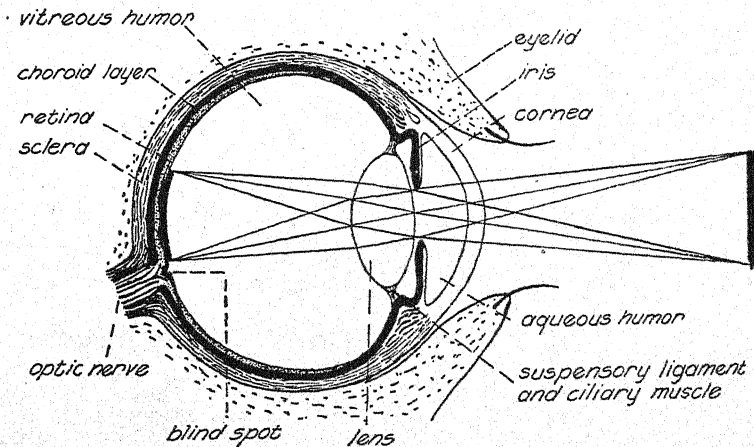


FIG. 34. The eye, in section, showing details of structure and also the manner of formation of an image upon the retina; diagrammatic.

(Adapted from C. Hill, "Manual of histology and organology," copyright, 1923, by W. B. Saunders Co., printed by permission.)

effectors served by the autonomic nerves are glands and muscles of blood vessels and coelomic viscera. The sympathetic nerve is one of the autonomic nerves (Fig. 33).

The Sense Organs. The sense organs, or receptors, of vertebrates are regions in which certain cells exhibit in a conspicuous manner the capacity of irritability in connection with particular changes in the environment. Organs of special sense, such as the eyes, ears, olfactory epithelium, and taste-buds, as well as the thermal and tactile organs, are located on or near the surface of the body. It is our purpose not to discuss the general structure of any of these organs but to call attention to their relations to the peripheral and central nervous systems. For example, the olfactory nerve extends from the olfactory epithelium of the nasal cavity to the brain, and the optic nerve passes from the retina of the eye to the brain (Figs. 33 and 34). The auditory nerve connects the sensory epithelium of the inner ear with the brain

(Fig. 35). In addition to the peripheral sense organs, there are sense organs in muscles and other internal organs.

The Skeletal and Muscular Systems. In a vertebrate animal the skeleton is internal and is called an *endoskeleton* in contrast to the external skeletons, or *exoskeletons*, which are found in many kinds of invertebrate animals. The skeleton of a vertebrate serves as a protective case for the central nervous system and as a rigid framework for the attachment of the muscles. Such a skeleton is composed of two

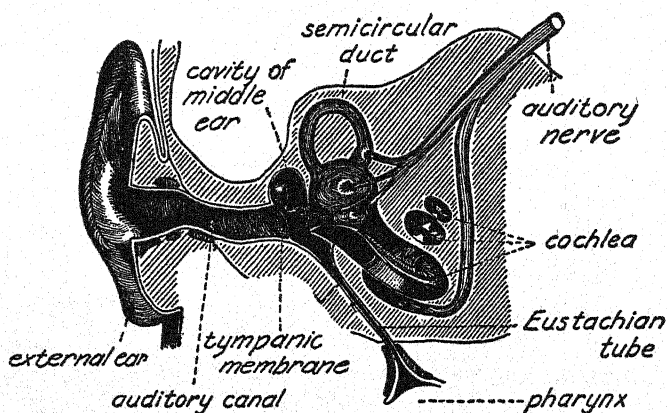


FIG. 35. The human ear; diagrammatic.

(From T. Hough and W. T. Sedgwick, "Human mechanism," copyright, 1918, by Ginn and Co., reprinted by permission.)

main parts, the axial and the appendicular skeletons (Figs. 36, 37, and 38). The *axial skeleton* includes the *skull*, which encloses the brain, and the *spinal* or *vertebral column*, which surrounds the spinal cord. Although the skeletons of different vertebrates vary in the number of bones making up the skull and the number of the *vertebræ*, as the bones of the spinal column are called, there is a striking uniformity in the fundamental plan. This uniformity is even more clearly shown in the fundamental plan of the *appendicular skeleton*, which is made up of the *shoulder* or *pectoral girdle*, the *hip* or *pelvic girdle*, and the bones of the *appendages*. The methods of locomotion in vertebrates are greatly diversified in correlation with the structure of the appendages. Fishes have paired fins which are ordinarily used for swimming but may be used for crawling on the bottom or gliding in the air. In air-breathing forms the typical five-toed limbs are modified for walking, burrowing, swimming, flying (cf. Figs. 487 and 488, pp. 668 and 669).

Locomotion is brought about as a result of the activities of the skeletal muscles, which are ordinarily referred to as the *muscular system*. *Muscles* are attached to rigid bones which are held together at the joints. By pulling against one another across joints, muscles make possible typical postures, as in man, and produce locomotion or move the appendages independently. *Joints* of the skeleton of the appendages

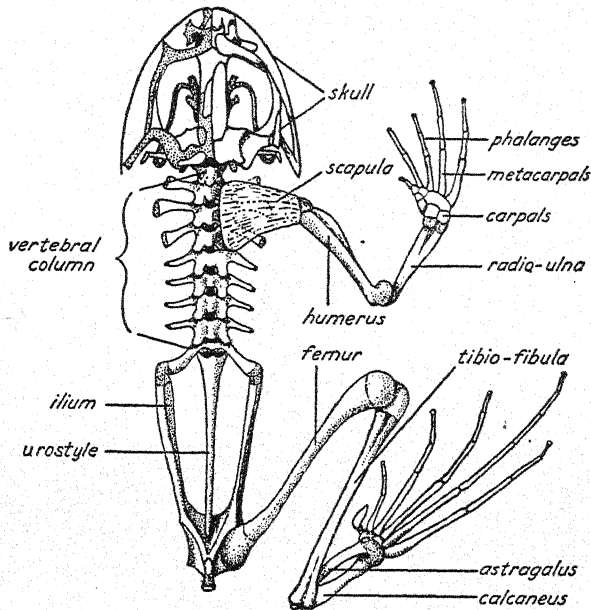


FIG. 36. Skeleton of frog, from dorsal view.

(Redrawn from T. J. Parker and W. A. Haswell, "Textbook of zoölogy," copyright, 1921, by Macmillan and Co., Ltd., printed by permission.)

are freely movable and of two main types. Hinge joints, which are found between the bones of the upper and lower arm and the upper and lower leg, allow movement in only one plane. Ball-and-socket joints, which are found where the bones of the upper arms articulate with the shoulder girdles and the bones of the upper legs articulate with the hip girdles, permit a rotation of the limbs when certain muscles contract or pull against others. The coördination of the activities of the muscles is extremely important for the animal as a whole and is brought about by the nervous system.

Nervous Coördination: Reflex Action. Every nervous coördination is the result of a reaction by some part of the body to a stimulus. The simplest type of response is that known as *reflex action*. When

you touch anything hot with your finger, the muscles of the arm react to withdraw the hand. Something passes from the point stimulated to the central nervous system and travels back to produce the contraction of the arm muscles. Another well-known illustration is the knee-jerk reflex, in which the leg is extended as a result of a sharp tap below

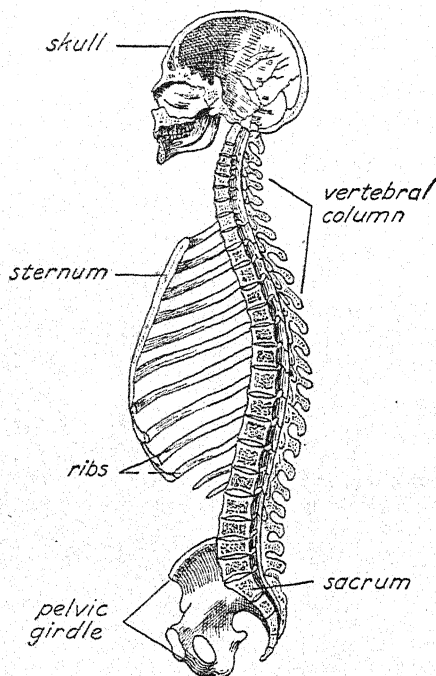


FIG. 37. Axial skeleton of man, in lateral view, with skull and vertebral column cut in median section.

(Redrawn from T. Hough and W. T. Sedgwick, "Human mechanism," copyright, 1918, by Ginn and Co., printed by permission.)

the knee-cap. In both these examples the response to the stimulus is apparent in the general region that receives the stimulus. This is somewhat comparable to the reflection of light by a mirror, in that the central nervous system seems to reflect the effect of the stimulus; the term reflex action is derived from the comparison. Complete analysis of these simple reflexes shows that they are the expression of a nervous mechanism which some investigators believe explains all nervous co-ordination.

The cells of the nervous system that are directly concerned with its function of coördination are known as *neurons*. Each has a nucleus

surrounded by a cytosome, or cell body, but the cytosome is conspicuously extended to form two or more processes (*cf.* Figs. 51 and 56, pp. 92 and 104). The neurons are arranged in such a way that the parts

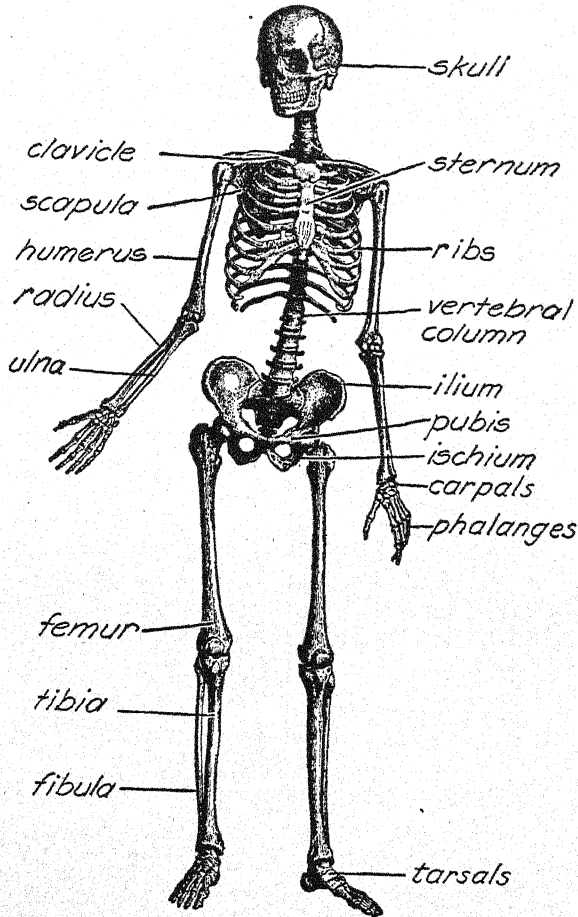


FIG. 38. Human skeleton.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

containing the nuclei are located in groups which constitute the *gray matter* of the central nervous system and the *ganglia* of the peripheral nervous system. The processes which are always continuous with the main part of the cytosome around the nucleus are sometimes called *nerve fibers*, and bundles of them make up the *white matter* of the central nervous system and the *nerves* of the peripheral system.

Neurons are arranged in what are known as *reflex arcs*, which are the cellular mechanism of reflex action. In a reflex arc a process from

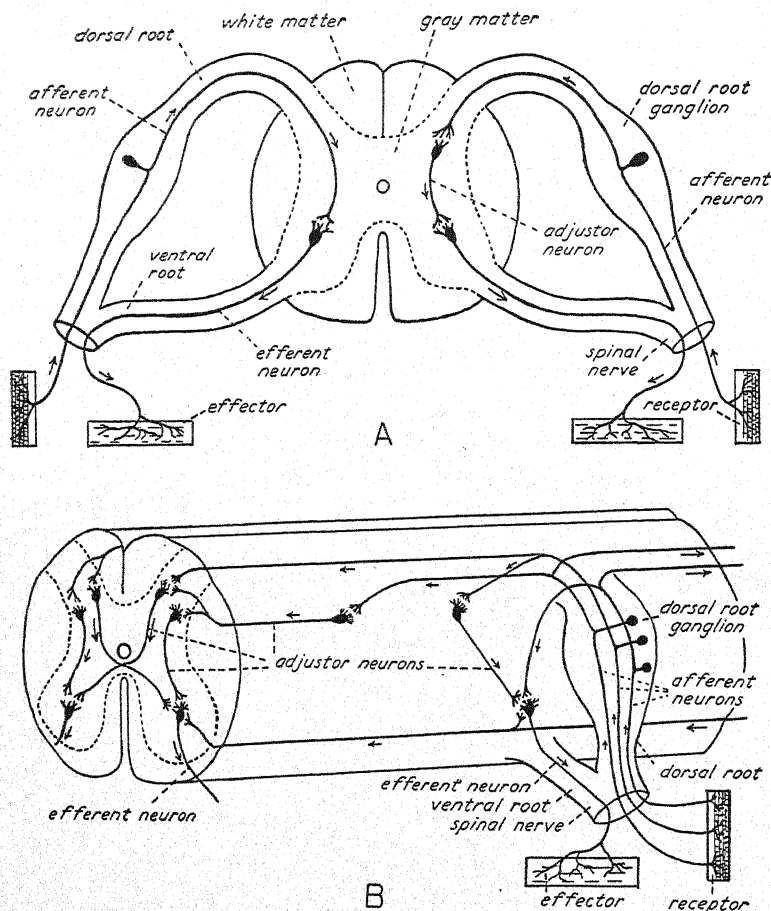


FIG. 39. *A*, the spinal cord, in cross-section, showing a pair of spinal nerves and the essential parts of a reflex arc; diagrammatic. The neurons necessary for the simplest type of reflex action are present on the left, while those of a typical reflex arc are represented on the right. *B*, the spinal cord showing some relations of neurons in reflex arcs; diagrammatic. The brain would lie to the right as the diagram is constructed. Arrows in both diagrams indicate the direction of transmission of the nervous impulses.

one neuron comes in contact with a process from another neuron, but no actual fusion occurs. Such places of contact between nerve-cell processes are known as *synapses* and make possible the functional

continuity of the nervous system. Extensions of one cell may have synapses with those of several other cells, so that nervous connections become very complicated, as will be shown later. However, in the simplest reflex arc there may be only two neurons involved (Fig. 39 A). The stimulus is received by some specialized group of cells constituting a *receptor*, which is a general term for any type of sense organ. As a result of the reception of the stimulus, what is known as a *nervous impulse* is established and transmitted from the place of stimulation toward the central nervous system along a nerve-cell process. In the simplest reflex arc the impulse will be transmitted to the spinal cord. The neuron over which the impulse enters the spinal cord is a *sensory* or *afferent neuron*. The cytosome of such a sensory neuron is located in the *dorsal root ganglion* of the *dorsal* or *sensory root* of a spinal nerve. One of the processes of the afferent neuron enters the centrally located gray matter of the spinal cord and comes in contact with processes of other nerve cells found there. In the case under consideration, the impulse would pass through the synapse between the process of the sensory neuron and one process of a *motor* or *efferent neuron* and leave the spinal cord by way of another process of the same efferent neuron which extends into the *ventral* or *motor root* of the spinal nerve. This process of the efferent neuron continues to a muscle cell, on which it terminates. The place of contact between a nerve-cell process and a muscle cell is known as a *neuro-muscular junction*, or *motor end-plate* (cf. Fig. 47). It is at such a place of contact that the impulse is discharged with the liberation of a specific chemical compound (cf. p. 86). The muscle cell is stimulated by this substance and reacts. This reaction is the effect produced by the stimulus received. A muscle is known, therefore, as the *effector* in the reflex arc. The parts of the simplest type of reflex arc are the receptor, where the stimulus is received; the afferent neuron, in which the impulse is set up and over which it is transmitted toward the spinal cord; the efferent neuron, over which the impulse passes away from the spinal cord and from which it is discharged; and the effector, where the reaction to the stimulus occurs.

When acid is applied to the skin on a frog's back, the first response is a contraction of the muscles of the body wall in that region. This is a simple reflex action. The receptor, in this example, consists of certain cells in the skin; the afferent neuron is one of the nerve cells lying in the dorsal root ganglion of the spinal nerve that supplies this particular region of the skin; the efferent neuron is one of the nerve cells of the gray matter of that part of the spinal cord to which the nerve passes; and the effector is a muscle cell of the body wall lying

under the region of stimulated skin. The knee-jerk reflex in man is perhaps even simpler. When the tendon of the muscle that extends the knee is tapped sharply just below the knee-cap, the stimulus is received by receptors in the tendon. The impulse is transmitted to the spinal cord over an afferent neuron and, passing through a synapse in the gray matter, travels back by way of an efferent neuron to a muscle cell. This effector, by its reaction to the discharge of the impulse, produces the extension of the knee. In both these examples the impulse is transmitted to an effector which is in the same region as the receptor. The analogy to light reflection is apparent.

In the great majority of reflex actions the effect is produced in some part of the body other than that at which the stimulus is received. If the skin of a dog's back is rubbed with a pointed implement, the animal will respond by attempting to scratch the place of stimulation with its hind leg. The receptors in this instance are located at the roots of the hairs of that region of the back which is stroked. The afferent neurons carry the impulse to the spinal cord over the dorsal root of the spinal nerve present in that region of the skin. Within the gray matter of the cord each sensory neuron has a synapse with a neuron of which both the cytosome and the processes lie entirely inside the spinal cord. Over the processes of such neurons the nervous impulse passes posteriorly along the spinal cord to the level of exit of the nerves that extend to the hind legs. Here synapses occur with efferent neurons, and the impulse leaves the spinal cord over the ventral root of a spinal nerve and passes to muscles (effectors) that produce the scratching motion.

In this type of reflex three neurons are concerned (Fig. 39 A). The neuron along which the impulse passes within the spinal cord is known as the *adjustor* or *internuncial neuron*. Adjustor neurons are very numerous in the central nervous system and make possible the varied reactions that a single stimulus can produce. For example, when acid is applied to the skin of a frog's back, the first reaction, as has been pointed out, is a contraction of the body-wall muscles in the region stimulated. Very soon, however, this is followed by other reactions which can be observed best in a frog from which the brain has been removed (Fig. 39 B). The fore leg on the side stimulated moves toward the location of the acid, and this reaction is followed quickly by movements of the hind leg on the same side. These movements tending to remove the acid are made possible by the passage of the impulse over adjustor neurons which transmit it anteriorly and posteriorly to efferent neurons leading to muscles of the fore and hind legs. The reactions described occur on the side of the animal to which the

acid has been applied. If under such conditions the hind leg that is moving is held, the muscles of the hind leg of the opposite side will respond to the original stimulus by contracting. This effect is made possible by the presence of adjustor neurons which carry impulses from one side of the spinal cord to the other and thus bring about bilateral coördination.

In the examples given we have been concerned with isolated reflexes; that is, particular reflex arcs have been discussed as if they were separable from the remainder of the nervous system. Such is obviously not the case. In fact, if any reflex reaction is analyzed completely, it is found to be dependent upon many reflex arcs. This compounding of reflexes, or the interaction between reflex arcs, is the principal method of nervous coördination. An organism at any particular moment is being subjected to many different kinds of stimuli, yet its reactions are orderly and correlated. If more than one reflex arc is activated at the same time, one of two things may happen. The reflexes may combine for the production of a harmonious effect, in which case they are called *allied reflexes*. In contrast to this condition, stimuli which occur simultaneously may not produce reflexes that reinforce one another. Instead, one of the reflexes may prevent the other from becoming effective, that is, may inhibit the other; such a reflex is said to be *antagonistic* with respect to the other. Series of reflexes, or their occurrence in sequence, are well understood in some situations and are a very important factor in reflex coördination. The procedure by which a frog obtains its food involves a sequence or *chain of reflexes*, which has been analyzed. The visual stimulus produced by a moving insect is followed by the protrusion of the tongue. If the insect is captured, its contact with the roof of the mouth cavity is the stimulus that results in the closing of the mouth. This, in turn, initiates the swallowing reflexes, which occur in sequence.

In the examples considered so far, the response to the stimulus has been studied with respect to the usual external conditions that produce the effect. Pavlov, a Russian physiologist, discovered that it is possible to produce what he termed *conditioned reflexes*. For instance, the flow of saliva is a reflex action stimulated normally by the sight of food. Under experimental conditions a bell is rung whenever food is given to an animal. After a number of such experiments the mere ringing of the bell, without the sight of food, will result in the secretion of saliva. In this way a stimulus that originally had no effect upon the salivary glands has become associated with one to which the glands respond. As a result of this association the previously indifferent stimulus of the ringing bell becomes effective in producing

the reaction of the salivary glands; a conditioned reflex has been established. Experiments and analysis of conditioned reflexes make it clear that many human reactions are the result of such correlations. Our responses to warning colors, signals, and nationally used signs and symbols are in the nature of conditioned reflexes. The same explanation holds for many more subtle and less well understood adjustments.

This compounding of simple reflexes into allied, antagonistic, and chain reflexes, any or all of which may apparently be conditioned, constitutes what is known as the behavior of the animal. The study of certain fields of animal reactions has indicated that behavior is dependent upon the pattern and order of the reflexes. *Pattern* is used to indicate the number of simple reflex arcs involved in the complex reactions and their localization in the nervous system. A study of pattern is essentially one of the morphology of behavior, or the tracing of possible pathways for the transmission of impulses. The study of order uncovers the time relations that exist in the succession of the simple reflexes. It is generally recognized that certain forms of behavior known as *instincts* are inherited. The nest-building and migratory instincts of birds, for instance, can be explained on the assumption that both the pattern and the order of the reflexes involved are inherited. Defense instincts of many young animals furnish other examples of inherited behavior. Reactions called *emotions*, such as fear, rage, and love, seem also to be illustrations of the inheritance of both pattern and order of reflexes.

The consideration of behavior also involves a discussion of *habit*. In habits both the pattern and the order of reflexes are acquired during the individual's lifetime. Habits of walking, dressing and undressing, eating, and talking are examples in which the pattern and order of reflexes may be determined very early in life. In learning to manipulate a machine one establishes reflexes of a particular kind and order. It takes only a superficial analysis of the routine procedure of operating an automobile or typing to trace the formation and seriation of the reflexes involved. Learning to perform any mechanical operation involves putting together a series of reflexes which may become a habit when it is finally established. The retention of habits involves memory. In any detailed discussion of behavior that takes account of the distinctions between emotions and instincts, the formation and retention of habits, and the interrelations that exist between these divisions, the student must follow the investigations and arguments of the psychologists in order to form his opinions. It can be said, however, with an increasing degree of certainty that analysis of

nervous coördination in all its complications depends on an understanding of the reflex arc.

The examples of reflex action that have been given are representative. It can be seen that, beginning with the simplest type of reflex arc in which one specific response occurs as the result of a stimulus, the series becomes increasingly complex as the result of the presence of one or many adjustor neurons between the afferent and efferent neurons. Both simple and complex reflexes may enter into allied and antagonistic combinations or form chains resulting in coördination. Patterns and orders of compound reflexes are transmitted from generation to generation and give rise to instinctive correlations. The mechanism of the reflex arc obviously makes possible the highest degree of coördination. Sherrington has generalized the facts of nervous coördination in his *principle of the common path*. Each afferent neuron is a special pathway by which impulses from its particular receptor enter the central nervous system. Within the central nervous system the impulse can travel over varied paths formed by synapses between adjustor neurons and, theoretically, can produce a reaction in any of the effectors. The efferent neurons, over which impulses travel from the central nervous system to the effectors, differ from the afferent neurons in that they are not private paths for particular impulses. It is a commonplace that many different kinds of stimuli can produce the same reaction or effect. Consider, for example, the many and varied stimuli to which man responds by walking. The efferent neuron is, therefore, a common path over which impulses established by stimulation of receptors all over the body can be discharged at a particular effector. By means of the adjustor neurons of the central nervous system, connections are made possible between all the special paths that lead from receptive areas and these final common pathways to effector regions. The transmission of impulses according to this principle of the common path establishes a mechanism for the complicated and varied responses that characterize nervous coördination. By means of this mechanism the animal is enabled to behave as a unit in its reactions to the changing conditions of its environment.

Localization of Function in the Nervous System. Up to this point nervous coördination has been analyzed in terms of the reflex arc. No particular emphasis has been placed on the position of the neurons involved in these arcs with reference to the morphology of the nervous system. It now becomes necessary to understand the functions of the different parts of the nervous system.

The general function of the *peripheral nervous system* is the transmission of nervous impulses to the central nervous system from recep-

tors and from the central nervous system to the effectors. In regard to the spinal nerves it has been pointed out that processes of afferent neurons enter the spinal cord over the dorsal roots of spinal nerves, and the processes of efferent neurons pass out along the ventral roots. The spinal nerves are called mixed nerves and may be considered to represent the primitive condition of nerve trunks. Certain of the cranial nerves, as the third or oculomotor, also carry processes of both sensory and motor neurons. Other cranial nerves carry processes of but one type of neuron. The eighth cranial or auditory nerve is made up entirely of processes of afferent neurons from the ear; the eleventh and twelfth cranial nerves, found in the higher vertebrates, contain processes of only efferent neurons. Finally, the autonomic nerves are entirely efferent and constitute the final common paths to glands and to the muscles of the blood vessels and viscera.

As has been repeatedly implied in the discussion of the reflex arc, the general function of the *central nervous system* is the adjustment of incoming to outgoing impulses. It is in the central system that afferent neurons have synapses with adjustor neurons and these in turn with efferent neurons. The multiplicity of connections thus made possible furnishes the most important part of the mechanism of integration. It is desirable to consider the nature of the adjustment in the different regions of the central nervous system (Fig. 40).

Adjustor neurons in the *spinal cord* are related to the simpler and less complicated of the reflex arcs. In the scratch reflex, for instance, adjustor neurons carry the impulse posteriorly in the spinal cord or transmit it from side to side. Impulses entering the cord over spinal nerves can also pass anteriorly to the medulla, cerebellum, and diencephalon. The cytosomes of these adjustor neurons are located in the gray matter of the spinal cord; their processes, over which impulses are transmitted along the cord, are to be found in the white matter. The white matter also contains groups of nerve processes which arise from the cell bodies of adjustor neurons located in the cerebral hemispheres, mesencephalon, and medulla. The gray matter of the cord is, therefore, the location of adjustor neurons which connect different levels of the cord with one another and with parts of the brain and which carry impulses from one side of the cord to the other. In addition, the cell bodies of efferent neurons, the processes of which pass out in the ventral roots of spinal nerves, are found in the gray matter of the cord. Simple reflexes are adjusted in the spinal cord, and impulses are transmitted to and from the brain.

The primitive brain, or brain stem, is composed of the telencephalon, diencephalon, mesencephalon, metencephalon, and myelencephalon.

Changes in the direction of greater brain complexity occur chiefly in the regions of the telencephalon and metencephalon, from which the

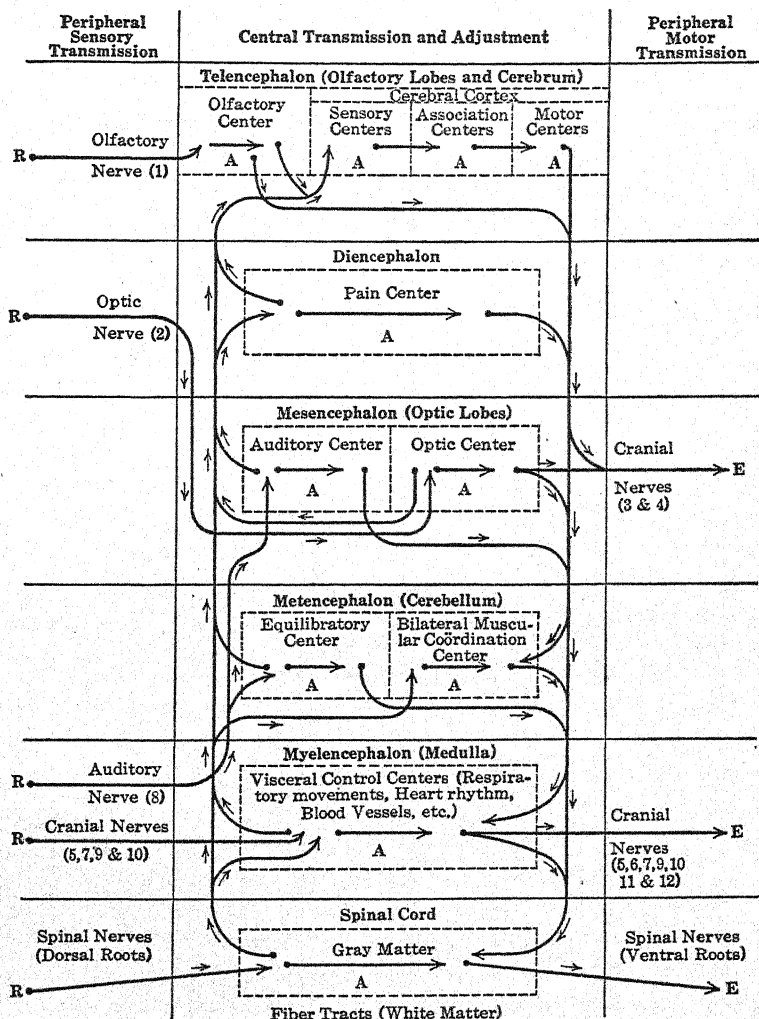


FIG. 40. Diagram to illustrate some of the possibilities of nervous coördination; no attempt is made to indicate specific reflex arcs. Impulses travel from receptors to the central nervous system and thence to effectors as indicated by the lines and arrows. A, adjustor neuron; E, effector; R, receptor.

cerebral hemispheres and the cerebellum, respectively, develop. The cerebral hemispheres and cerebellum are the parts in which new functions are added; the functions of the brain stem remain practically

constant throughout the vertebrate group. In contrast to its arrangement as a column in the spinal cord, the gray matter occurs in the brain in masses known as *centers*, which may be surrounded completely by white matter, as in the medulla, or form a continuous peripheral layer, as in the cerebral cortex (Fig. 41). It is impossible

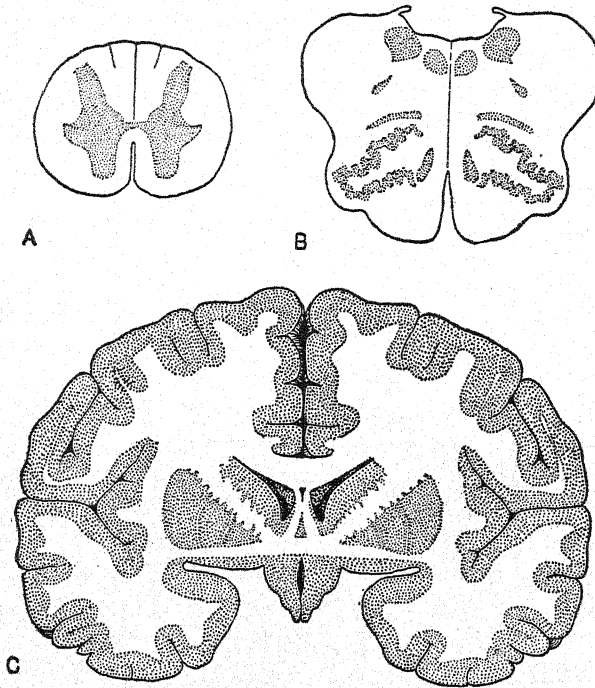


FIG. 41. Different regions of the central nervous system, in cross-section, to show the distribution of white (clear) and gray (stippled) matter; diagrammatic. A, spinal cord; B, medulla; C, cerebral hemispheres.

to present here a detailed account of the functions of the parts of the brain, but the more important localizations will be given.

The *medulla*, into which the spinal cord merges, serves as a pathway between the cord and other parts of the brain. It also contains the centers that adjust the reflexes of the tongue and of breathing. In the tongue reflexes, impulses enter over processes of afferent neurons by way of the fifth and ninth cranial nerves and pass out over processes of efferent neurons by way of the twelfth nerve. The adjustor neurons lie in centers within the medulla. The respiratory reflex depends upon the sensitivity of the respiratory center in the medulla to the amount of carbon dioxide in the blood. Impulses

are transmitted over processes of efferent neurons to muscles between the ribs and in the diaphragm. The rhythm of breathing and other reflexes of the viscera, pharynx, and larynx are also adjusted in the medulla.

The ventral part of the *metencephalon* consists of fiber tracts that transmit from side to side, as well as of those connecting lower and higher levels. In the *cerebellum*, or dorsal part of the metencephalon, there are important muscle-coördinating centers. These coördinations may involve the body as a whole, as when reactions occur in response to stimuli received by the organs of equilibration, the semicircular ducts of the ear. The adjustments that result in bilateral muscular coördinations are also made in the cerebellum. Such bilateral coördinations are chiefly those of the movements of the limbs, although the muscles of the eyes, facial expression, and mastication are believed by some investigators to be bilaterally correlated in cerebellar centers.

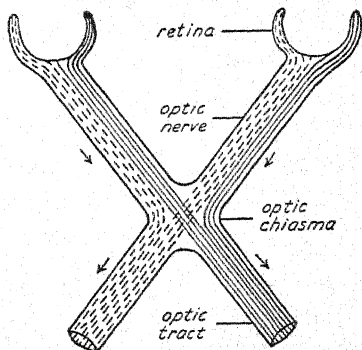


FIG. 42. The optic chiasma in higher vertebrates; diagrammatic.

On the dorsal surface of the *mesencephalon* are found the *optic lobes*, where centers are located in which certain important visual reflexes, such as the constriction of the pupil of the eye in response to the stimulus of light on the retina, are adjusted. In the higher vertebrates certain reflexes following sound stimuli are also adjusted in the optic lobes. The lateral and ventral regions of the mesencephalon contain groups of neurons that provide for numerous connections and nerve tracts over which impulses are relayed from one region to another.

In the *diencephalon* many nerve tracts connecting centers in other parts of the brain with the cerebral cortex are found. The optic nerves and tracts over which impulses travel from the retinas to the optic lobes form the floor and part of the lateral walls of the diencephalon (Fig. 32 C). In the lower vertebrates all the fibers from one retina cross the optic chiasma to enter the opposite optic lobe. The crossing in higher vertebrates involves only the medial half of the fibers of each retina; the fibers of the lateral halves do not cross (Fig. 42). Certain correlations resulting from olfactory stimuli are made in the diencephalon, and impulses giving rise to pain sensa-

tions are received there. Other centers are important relay stations in the compounding of reflexes.

Among the lower vertebrates the most important parts of the *telencephalon* are the centers for correlation of impulses transmitted from the olfactory organs. The olfactory centers in mammals occupy the same relative position but are overshadowed by the very great growth of the dorsal part of the telencephalon to form the *cerebral hemispheres*. In the cerebral hemispheres, as in the cerebellum, the neurons that make up the gray matter are found in a continuous superficial layer known here as the cerebral cortex. Although the cortex is continuous, certain areas are known to be concerned with special functions. Impulses producing movements of the voluntary muscles are transmitted from the motor centers of the cortex to opposite sides of the body; that is, if these particular areas are destroyed in one cerebral hemisphere, the animal is unable to use the voluntary muscles on the opposite side of the body. The regions that coördinate movements of the principal parts of the body, from the toes to the face muscles, are known in man (Fig. 43). Another major division of the cortex is concerned with sensory functions and contains the sensory centers to which impulses are transmitted from visual, auditory, and olfactory receptors, as well as from receptors of pressure, temperature, and taste stimuli. These areas have been mapped almost completely for the human cortex. The association centers of the cortex are filled with adjustor neurons which are involved in the complicated pathways used in the mental activities of thinking and learning.

Intelligence is dependent upon the degree of development of the cerebral cortex and especially upon the neurons of the association areas. An animal's ability to profit by experience involves analysis of a situation and memory, enabling the individual to react in a way that is advantageous in a new situation. This ability is determined by the animal's degree of intelligence, which, in turn, is limited by the number of adjustor neurons and the synapses existing between them. It is known that all the neurons that an animal will ever possess are present at a very early stage of its development. New synapses are, however, formed throughout the life of the individual and probably depend upon the variety and intensity of the stimuli received by that individual. The sensory impulses that reach the cerebral cortex, the motor impulses that pass out from it, and the associations made in it constitute our so-called consciousness. Sleep and anesthetics in some way lessen or completely block the functioning of the cerebral cortex and produce unconsciousness. It is sometimes

said that the cerebrum initiates or controls voluntary movements. This is not the place to enter upon a discussion of the will, but it must be stated that, so far as the function of the nervous system is understood, the neurons of the cerebrum transmit impulses set up in response to stimuli, just as the neurons do in other parts of the central nervous system. The sources of the stimuli may be difficult to locate, but

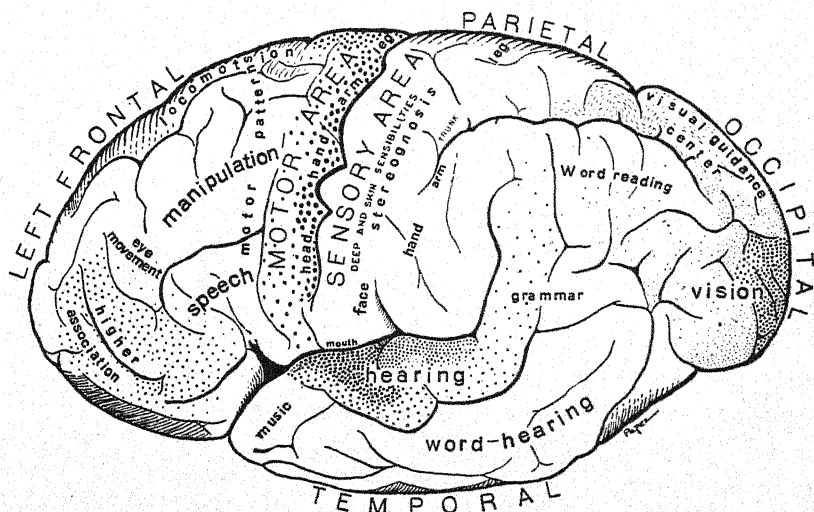


FIG. 43. The left cerebral hemisphere of the human brain, on which the subdivisions of the sensory and motor areas are indicated, as well as the location of the higher association centers.

(From J. W. Papez, "Comparative neurology," copyright, 1929, by Thomas Y. Crowell Co., reprinted by permission.)

that reason does not seem to be sufficient for departing from the conception of a neuron mechanism.

In summary of the details of functional localization, the central nervous system has the general function of adjustment of impulses, while the peripheral nervous system furnishes transmission paths between all parts of the body and the central nervous system. By the combined functions of the nervous system as a whole, the activities of the organism are correlated so that it behaves as a unit; the function of the nervous system is, therefore, coördination or integration. The degree of integration of which an animal is capable determines its ability to react successfully to its environment; this is a very important factor in its survival. The increase in the complexity and specialization of the nervous system has, therefore, been said to be one

of the chief factors in evolution. As Gaskell puts it, "The law of progress is this: The race is not to the swift, nor to the strong, but to the wise."

Reception, Transmission, and Discharge. It has been pointed out that nervous coördination depends essentially upon three factors. In the first place, the organism must be able to be aware of changes in its environment, that is, to receive stimuli. Second, nervous impulses which are set up in nerve-cell processes in response to the stimulus are transmitted over reflex arcs. And, finally, the animal responds to the stimulus when the impulse is discharged at some effector. Theories of reception, transmission, and discharge are rather complicated, and the processes are not well understood. However, certain statements on these subjects can be made.

Animals like the vertebrates possess sense organs which are specialized for the reception of stimuli. These sensory areas, or receptors, respond to special kinds of stimuli. The retina of the eye is a receptor for changes in the environment brought about by light waves (Figs. 44 and 45). In the lower fishes the ear is primarily a receptor for stimuli produced by changes in the animal's position. As a result, the animal maintains or resumes a typical position with respect to its surroundings. The semicircular ducts of the ear in higher vertebrates retain this function of equilibration, while the cochlea becomes sensitive to sound waves (Fig. 35). Chemical substances in solution stimulate the olfactory epithelium of the nose and the taste-buds of the mouth (Fig. 46). Certain areas of the skin are sensitive to changes in temperature, others to touch. The nature of the specialization involved in receptor surfaces is not understood, but their specificity is well known. Sound waves do not start an impulse in the retina. On the other hand, if the optic nerve is stimulated mechanically, the impulse that is initiated results in a visual sensation. The person who says he "sees stars" when he gets a "black eye" has scientific foundation for his assertion. Receptors normally are sensitive to only one type of stimulus, but, if they can be stimulated by unusual methods, the impulse produces the typical sensation.

The reception of a stimulus by a sensory area is followed by the establishment of a nervous impulse and its transmission along the processes of the afferent neurons associated with the area. Nerves were at first thought to be tubes that conducted the "animal spirits," which were supposed to be like gas. Later, the material carried by the tube was believed to be more like water and was called "animal juice." The nature of the nervous impulse and its transmission still remain a puzzle in many respects and engage the attention of many investi-

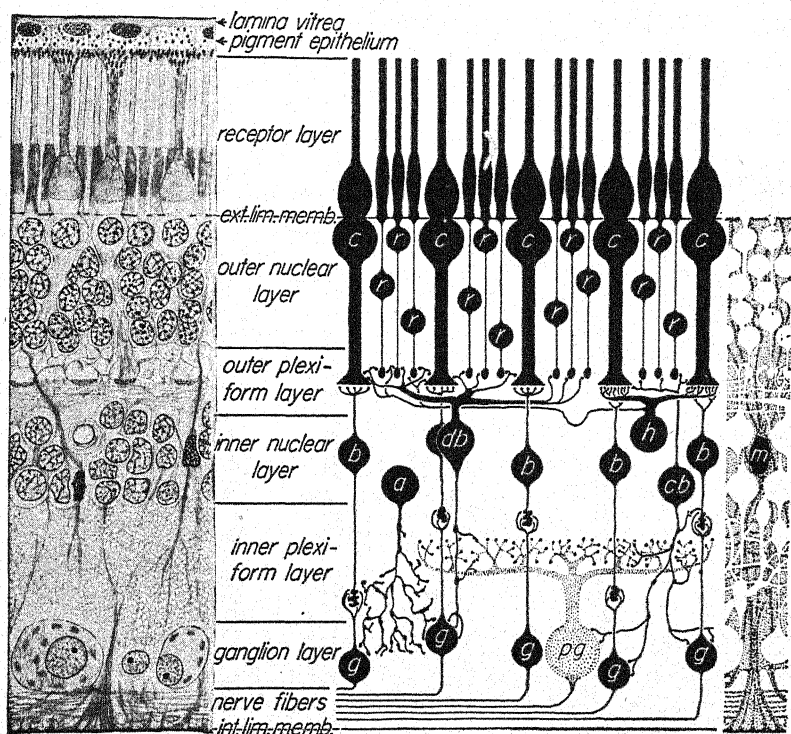


FIG. 44. The human retina. *Left*, drawing of vertical section; the region at the bottom is adjacent to the chamber of the vitreous humor; $\times 500$. *Middle*, diagram showing relationships of principal types of cells. Light passing through the lens, vitreous humor, and inner layers of the transparent retina reaches the receptor layer made up of the outer segments (*cf.* Fig. 45), or photosensitive regions, of the cones (*c*) and rods (*r*). Nervous impulses established in the region called the outer plexiform layer are transmitted by way of neurons of different types, the cell bodies of which are shown at *a*, *b*, *cb*, *db*, *g*, *h*, and *pg*. These impulses finally are transmitted by way of the nerve fibers which form the innermost layer of the retina and which extend outward through the retina in the region of the blind spot (*cf.* Fig. 34) to make up the optic nerve. *Right*, diagram of a Müller fiber (nucleus at *M*), which functions to hold the other retinal elements together; opposite ends of the Müller fibers form the external limiting membrane (*ext. lim. memb.*) and the internal limiting membrane (*int. lim. memb.*), which lies adjacent to the vitreous humor (*cf.* Fig. 34).

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gators. Some workers have believed that the transmission of the nervous impulse is the result of chemical reactions along the nerve process. The analogy to the burning of a path of gunpowder is some-

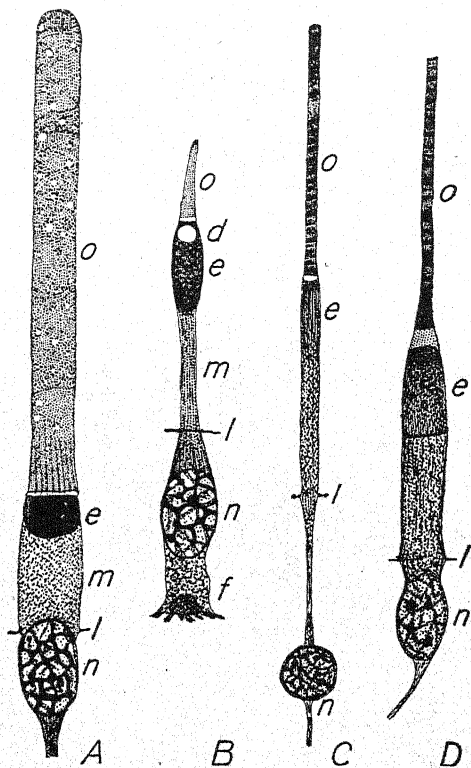


FIG. 45. Visual cells of vertebrates; $\times 1000$. *A*, common rod of leopard frog; *B*, common cone of leopard frog; *C*, rod of man; and *D*, cone of man. *d*, oil droplet, typically embedded in *e*, the ellipsoid, which is probably a light-concentrating region; *f*, the foot-piece which makes contact with dendrites of nerve cells in the outer plexiform layer (cf. Fig. 44); *l*, position of external limiting membrane (cf. Fig. 44); *m*, myoid, a contractile region not present in human visual cells; *n*, nucleus; *o*, outer segment or light-sensitive portion.

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times made. This idea involves a conception of dissimilative metabolic activities in the neuron process. Such metabolism uses oxygen and produces carbon dioxide and heat. The production of carbon dioxide and heat in sufficient quantities to justify a chemical interpretation of nervous transmission has not been demonstrated. The fact

that it is almost impossible to detect in a nerve signs of fatigue or loss of capacity to transmit is also an argument against the metabolic theory. Opposed to the chemical interpretation is a physical theory which explains transmission in terms of the passing of an electric current. The velocity of nervous transmission varies from 27 to 125 meters (about 88 to 406 feet) per second in the cases measured. This rate is, of course, much slower than that of electrical transmission through metals or air. That an electric current occurs simultaneously with the transmission of an impulse has been clearly established,

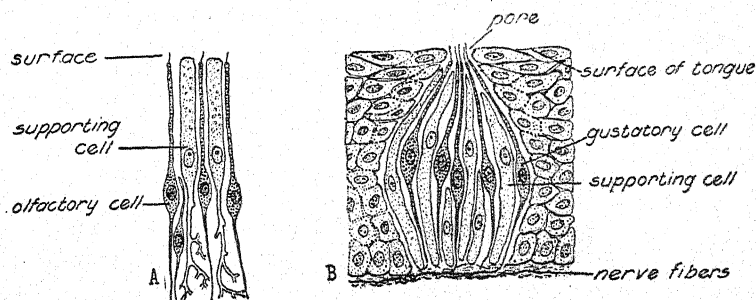


FIG. 46. A, cells of olfactory epithelium from the human nose. B, cells of a taste-bud in epithelium of the tongue. In both cases, the sensory cells terminate externally in hairlike processes that are able to receive the chemical stimuli of olfaction, or smell, and gustation, or taste, respectively.

although it must be granted that such a demonstration does not prove that they are one and the same. It may well be that the transmission of a nervous impulse is dependent upon both chemical and physical factors.

An interesting feature of transmission is that the direction of conduction in the nerve cell is not reversible. Afferent neurons always carry impulses toward the central nervous system; efferent neurons always carry impulses away from the central nervous system. No fundamental difference in the morphology of afferent and efferent neurons has been found. The statement has been made that it is impossible to fatigue a nerve process, that is, to diminish its capacity to transmit impulses. However, fatigue occurs when the impulse is permitted to pass over the entire reflex arc and produce an effect. Transmission through the central nervous system involves transmission through the synapses that connect neurons. The evidence indicates that changes occurring in the synapses are responsible for the fatigue.

Apparently, when a nervous impulse reaches the end of any nerve fiber, the brushlike terminal filaments secrete a chemical substance

known as a *neurohumor*. If the endings of the nerve fiber are in contact with other nerve fibers, as in a synapse, this neurohumor sets up an impulse in a new fiber. Where the fiber ends in contact with an effector, a motor end-plate, or neuro-muscular junction, occurs (Fig. 47). It is in such regions that the so-called discharge of the nervous impulse takes place. The release of the neurohumor by the terminal brush of the fiber constitutes a change in the environment of the effector, and it responds to this stimulus by reacting. In the skeletal

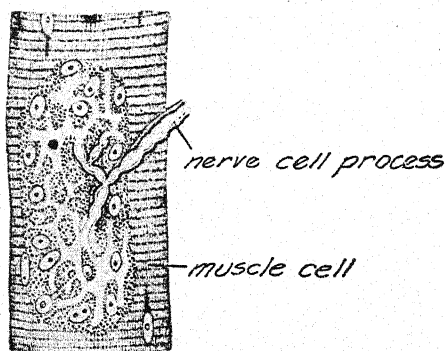


FIG. 47. Neuro-muscular junction between a nerve-cell process and a striated muscle cell.

(From E. A. S. Schäfer, "Essentials of histology," copyright, 1916, by Longmans, Green and Co., reprinted by permission.)

muscle the reaction is a contraction; the muscle is said to have been excited. If, now, heart muscle is considered, it is observed that impulses reaching it over an autonomic branch from the vagus nerve slow its rate of contraction, that is, tend to inhibit it. Impulses reaching the heart over a branch from the sympathetic trunk increase its rate of contraction, or excite it. The difference in type of response in the heart, that is, excitation versus inhibition, and in other parts of the body innervated by the autonomic nerves is explainable in terms of the neurohumors. From the ends of efferent fibers on skeletal muscle and probably from all other fibers, with a single exception to be referred to soon, a neurohumor known as acetylcholine is secreted. The terminal brushes of fibers that reach effectors by way of the sympathetic nerves of the autonomic group secrete a neurohumor known as adrenalin (*cf.* p. 58). An effector is excited by one of these substances and inhibited by the other. This is the mechanism of nervous control of involuntary responses.

Summary

It must not be forgotten that coördination in any organism depends in the last analysis upon the irritability of protoplasm. The unicellular animals respond directly to stimuli which are received and become effective in the protoplasm of the same cell. That the individual cells of multicellular organisms retain the capacity to respond directly to changes in their immediate surroundings is clear from the nature of chemical coördination, in which hormones carried in the blood and lymph produce reactions by direct stimulation. However, it is impossible for each cell in a highly organized multicellular animal to be stimulated directly by changes in the environment of the organism as a whole. Integration of the many-celled animal is accomplished by means of the mechanism of the neuron arcs of the nervous system, connecting receptors and effectors according to the principle of the common path. This coördination of higher forms is associated with great specialization of cells and regions. A particular receptor receives only a certain kind of stimulus; neurons conduct impulses in only one direction; and effectors respond in a distinctive manner to discharged impulses. The question of the fundamental nature of this specialization cannot be answered at present. Nor, for that matter, can the essential character of irritability be explained clearly. Certain facts point to a close association between metabolism and irritability. In other words, if the metabolism of a cell is altered, its irritability will be changed. Metabolism, in turn, depends upon the physico-chemical nature of protoplasm. The complete explanation of irritability and coördination, therefore, awaits further knowledge of the nature of protoplasm. It is quite possible, however, to understand to a greater or lesser degree the outward expressions of protoplasmic irritability which are observed in the behavior of animals. The functions of specialized organs and systems are coördinated in such a way that the organism behaves as a unit, a physiologically balanced individual potentially able to maintain itself in the struggle for existence.

CHAPTER 4

STRUCTURE AND ACTIVITIES OF CELLS IN MULTICELLULAR ANIMALS

The account of the various organ-systems of the vertebrates has brought out the fact that the metabolic requirements of protoplasm are satisfied only when certain of these systems perform their specialized functions. The coördinating systems, on the other hand, make possible the working together of all parts of the body as a result of the response of protoplasm to changes in its environment. It is evident that the outward manifestations of life by the organism have significance if they are related to the capacities of living protoplasm contained in its cells. These masses of protoplasm are extremely important not only in connection with the capacities of metabolism and irritability but also in relation to reproduction, development, and heredity. In this chapter the different kinds of cells and some of their fundamental activities will be described.

The Cell Theory

The discovery of cells was made possible by the use of the microscope, which was invented about 1591 but was not utilized in scientific studies until about 1650 (Fig. 48). Robert Hooke, one of the early English microscopists, discovered that cork is composed of small spaces surrounded by firm walls, and in 1665 he named these compartments *cells* (Fig. 49). The development of microscopic instruments was very slow, and it was not until 1833 that Robert Brown observed in certain plant structures that each cell contains a small body which he called the *nucleus*. In 1838 Schleiden, a German botanist, proposed the interpretation that cells are the units of structure in plants; and Schwann, a German zoölogist, extended this conception to the structure of animals in 1839 (Fig. 50). This was the first formulation of the *Cell Theory*. The founders of this theory and other biologists of that time believed that the walls that surrounded plant cells were the essential parts of these units. The contents of cells had

been observed but were regarded as unimportant or as waste products. Purkinje in 1840 and von Mohl in 1846 gave the name *protoplasm* to the cell contents. Through a series of researches it became appar-

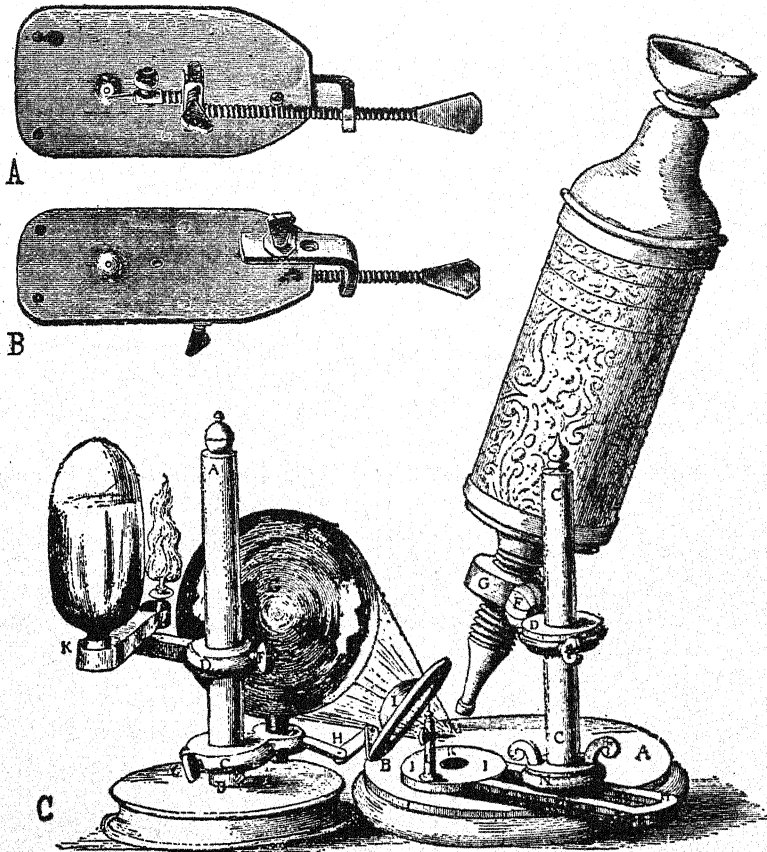


FIG. 48. *A* and *B*, different views of Leeuwenhoek's microscope (about 1673). *C*, Hooke's compound microscope, showing method of illumination (1665). (From W. B. Carpenter, "The microscope and its revelations," copyright, 1891, by J. and A. Churchill, reprinted by permission.)

ent that protoplasm was the essential part of cells; walls were found only around plant cells. Likewise, a nucleus was found to be present in almost all types of cells, and a cell came to be defined as a mass of protoplasm containing a nucleus.

As knowledge became more complete, it was ascertained that in certain parts of the animal much non-cellular material lies between

cells. This material, examples of which will be given later, was shown to be produced by cells, and the Cell Theory was modified by saying that organisms are composed of structural units, called cells, and of cell products. Further study of animals with reference to their activities has revealed the fact that all physiological processes must be understood in terms of the functions of cells; that is, the cell is the unit of function. The Cell Theory has, therefore, been extended and confirmed, and it now stands as one of the fundamental generalizations of biological science. A complete statement of this unifying conception of biology would be that all living organisms are composed of

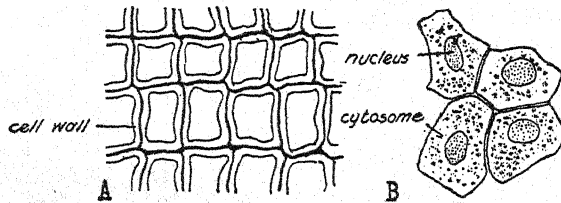


FIG. 49. *A*, cork, showing the cell walls characteristic of plant cells; diagrammatic. *B*, squamous epithelium, showing nucleus and cytosome in animal cells; there are no cell walls.

cells, which are the units of structure and function, and of cell products. In complex organisms these units are not independent but are coordinated by their own activities, so that the animal as a whole may also be regarded as a unit. This obvious fact of interrelation between the cells of an individual is sometimes emphasized in what is called the *Organismal Theory*. In the final analysis the organism is regarded as a protoplasmic unit according to this theory, and there is no essential difference between it and the modern interpretation of the Cell Theory, which is much easier to use in understanding the structure and function of an animal.

A Composite Cell. A cell may be correctly defined, in a general way, as a mass of protoplasm containing a nucleus. However, certain cells, notably the red blood cells of mammals, lose their nuclei during their differentiation; others, such as striated muscle cells, contain many nuclei. If the definition is to hold for all cases, it must be modified to state that a cell is a mass of protoplasm which contains one or more nuclei at some stage in its differentiation. This statement, together with the definition of a cell as the unit of structure and function, is of fundamental importance in the further consideration of cells. Structurally, cells are divided into two main parts, the *cytosome*, or cell body, and the *nucleus*. In the following account these parts will be

considered as they occur in what may be called a composite cell which is not dividing (Fig. 51); that is, all the parts that can be identified in many different kinds of cells are described in a single cell.

The cytosome contains *protoplasm*, or *cytoplasm* as it is often called, and is limited externally by the *cell membrane*, or *plasma membrane*, which is the outermost cytoplasm of the cell. A number of structures can be distinguished in the cytosome, where they are surrounded by the cytoplasm. Lying near the nucleus is a differen-

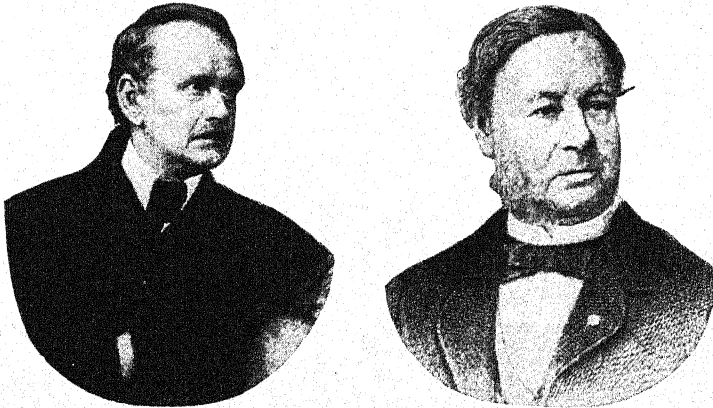


Fig. 50. *Left*, Matthias Jacob Schleiden, 1804-1881; *right*, Theodor Schwann, 1810-1882.

(From W. A. Locy, "Biology and its makers," copyright, 1908, by Henry Holt and Co., reprinted by permission.)

tiated, rounded area of cytoplasm, the *centrosphere*, which encloses one or two small granules, the *centrioles*. The centrioles are conspicuous structures during the process of mitotic nuclear division (*cf.* p. 107). A number of different kinds of bodies found more or less commonly in the cytosome are grouped under the name of *cytoplasmic inclusions*. *Chondriosomes* are the most universal members of this group. These are usually small granules, isolated or arranged in rows; they are typically scattered throughout the cytosome but may be more numerous in some regions than in others. *Golgi elements* have been observed in many cells. *Fat* is stored frequently as larger or smaller drops. *Yolk* is found in the form of plates or spheres in egg cells. In many cells *vesicles* filled with solutions of unknown composition are present. When the contents of these vesicles are lost, they may appear as vacuoles. Secretions produced in gland cells are often stored as *secretion granules* until they are passed from the cells. The cytoplasmic inclusions constitute a diversified group, but all can

be understood in terms of the activities of the protoplasm which surrounds them; they are the visible products of certain metabolic activities of protoplasm, stored until used or discharged from the cell.

The nucleus, which is usually round and somewhat centrally located, is everywhere surrounded by the cytosome and separated from it by a continuous membrane, the *nuclear membrane*. The most con-

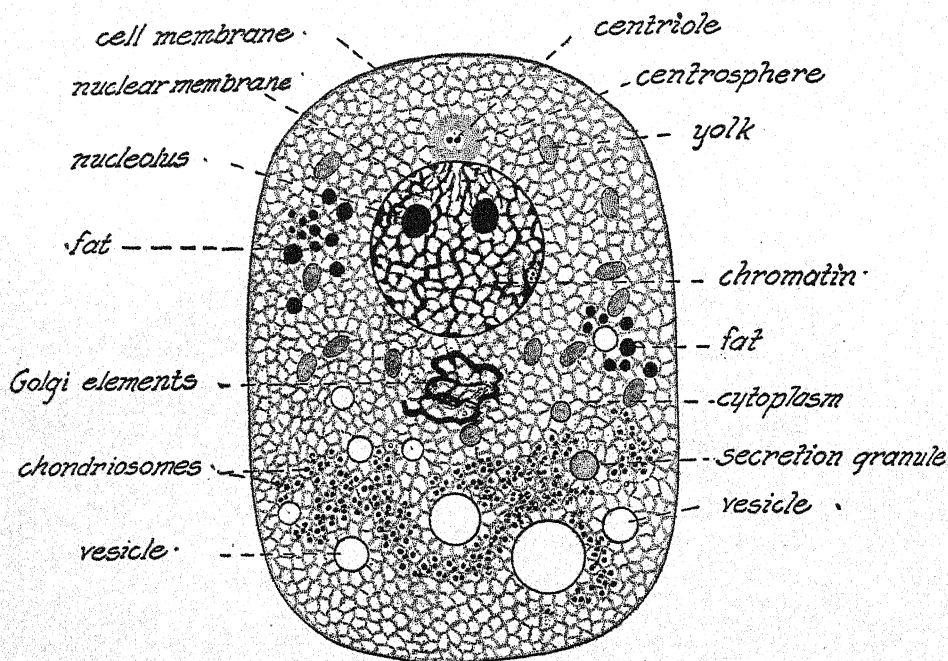


FIG. 51. A composite animal cell in the vegetative phase; diagrammatic.

spicuous material in the nucleus is the *chromatin*, so called because it can be intensely colored with some stains during mitosis. Chromatin frequently appears to exist as isolated granules, but modern studies increasingly indicate that these granules are really thicker regions of delicate threads called chromonemata. Recognized in 1908 by Kristine Bonnevie in *Ascaris* and one of the amphibians, these threads were later studied in plant chromosomes by Sharp and Nebel (Fig. 59). The behavior of chromatin threads and masses in the activities of cell division and the differentiation of germ cells is important in connection with the mechanism of heredity and will be considered later. One or more *nucleoli*, which are typically round, are always present. They are perhaps best interpreted as temporary storage products of nuclear metabolism and have been shown to be produced by certain

regions of particular chromosomes. Surrounding the chromatin and the nucleoli is the nucleoplasm, sometimes called nuclear sap. Both nucleus and cytosome are necessary for the normal activities of the cell. It is not possible to define exactly the part each plays in the metabolism of the whole. Cells that are deprived of their nuclei are unable to carry on assimilation, although dissimilation goes on until the cytoplasm is exhausted. This fact and other types of experimental evidence would seem to indicate that the nucleus may be a place where enzymes necessary for assimilation are produced, and that the cytosome is the principal region of synthetic activity and energy transformation in the cell. Whether or not such a distinction can be sharply drawn, it cannot be doubted that there is very close interdependence between the two morphological divisions and that the life of the cell depends upon balanced interactions between nucleus and cytosome.

Histology

In the preceding section a so-called composite cell has been described. If the body of a vertebrate is examined microscopically, no cell will be found that conforms to this account; cells differ among themselves, although they all possess certain features in common. Cells may be dissimilar in shape, position in the body, structure, and also in function. Cells that are similar in structure and function make up groups known as tissues; *tissues* are groups of cells specialized in the same way for the performance of the same function. Tissues are associated to form the *organs* that perform special functions. The cells as they are grouped to form tissues and organs must be studied by means of the microscope. This particular study of structure is known as *histology*, or microscopic anatomy, in contrast to gross anatomy, or the study of the organ-systems by dissection. If we consider tissues first, we find that they are classified according to structure and function. There are five principal classes of tissue: epithelial, sustentative, vascular, contractile, and nervous.

Epithelial Tissue. The cells of epithelial tissues are compactly placed with but a small amount of intercellular material. Their functions include the covering and protection of body surfaces, both internal and external, as well as absorption, secretion, and excretion. According to the predominating shape of the cells; this class is subdivided into *squamous* and *columnar epithelium*, each of which is again divided into *simple* or *stratified*, depending upon whether it exists in single or multiple layers. The cells of simple squamous epithelium when viewed from the surface resemble tiling-blocks; seen from

the edge, they are very thin (Fig. 52 A). Such epithelium is found lining the coelom; that is, it forms the peritoneum (Fig. 52 B). In stratified squamous epithelium only the outermost layers are typically flattened cells; in the deeper layers the cells are progressively more cuboidal (Fig. 52 C). Since blood vessels do not penetrate epithelial

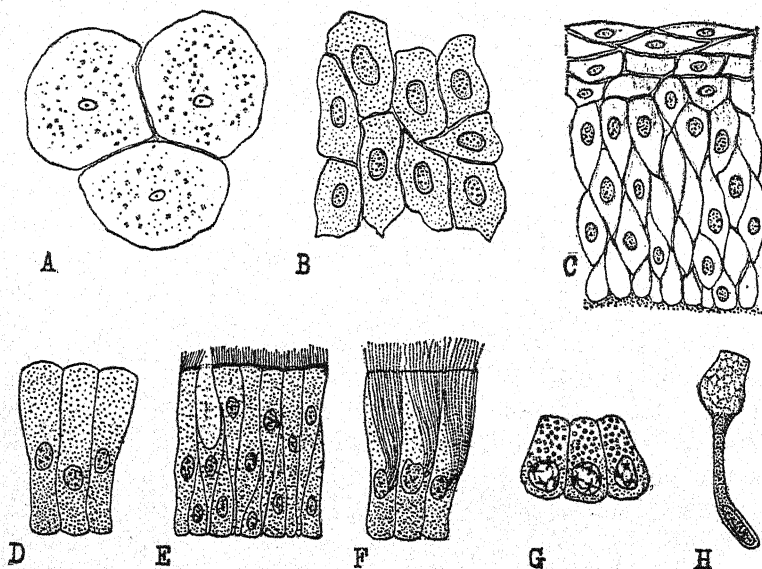


FIG. 52. Epithelial tissues. *A*, simple squamous epithelium from the human mouth. *B*, simple squamous epithelium (mesothelium) from peritoneum. *C*, stratified squamous epithelium from the lining of the nasal cavity. *D*, simple columnar epithelium from the mucous membrane of the digestive tract. *E*, pseudostratified ciliated columnar epithelium from the lining of the trachea; one cell is shown secreting a drop of mucus. *F*, simple ciliated columnar epithelium. *G*, glandular epithelium from the pancreas. *H*, goblet cell with a drop of mucus. *A* and *B*, surface views; *C*-*H*, sections at right angles to surfaces which are toward the top of the page.

(*A*, *B*, and *C* from drawings by D. F. Robertson.)

layers, only the cells of the deeper layers receive abundant nourishment and consequently divide and replenish the outer layers, which die and are cast off. Stratified squamous epithelium is found in the outer layer, or epidermis, of the skin and in the lining of the nasal and mouth cavities, pharynx, and esophagus of many vertebrates. In simple columnar epithelium, such as that lining most of the digestive tract, the cells are longer than they are wide and are arranged side by side (Fig. 52 D). Stratified columnar epithelium is not com-

mon, but a modified type is found lining the trachea (Fig. 52 E). Columnar epithelial cells sometimes have their free surfaces, that is, the surfaces exposed to the cavity that they line, covered with cilia, which are hairlike cytoplasmic processes (Fig. 52 F). The cilia are vibratile, and their motion removes any foreign materials from the surfaces. The epithelium of the air passages in higher vertebrates and of the roof of the frog's mouth is an example of this variation (Fig. 52 E). In the iris and retina of the eye, epithelial cells contain pigment granules and are known as pigmented epithelium; in organs of secretion, columnar epithelium, specialized for the production of certain types of secretions, is known as glandular epithelium (Fig. 52 G). Epithelial cells, temporarily modified as gland cells, occur as "goblet cells" (Fig. 52 H), so called because they are distended by a drop of secretion in the epithelial lining of the digestive tract.

Sustentative Tissue. The sustentative tissues, often called the connective tissues, are a very heterogeneous group, classed together because they are all derived during development from the same source—the stellate mesenchyme cells (Fig. 53 B). In general, sustentative tissues function in supporting the body and connecting or binding together its parts. This group of tissues is characterized by the large amount of intercellular material which is produced by the cells. In the vertebrates this intercellular material is responsible for the supporting and connecting qualities. Sustentative tissue may be divided into four subclasses: connective tissue in the restricted sense, cartilage, bone, and adipose tissue.

Connective tissues are of three kinds: *mucous connective tissue*, in which the intercellular material is gelatinous, is found in the umbilical cords of mammals (Fig. 53 A); *reticular connective tissue*, in which there is a meshwork of connective tissue cells with the interspaces filled with other types of cells, forms the framework of organs like the spleen (Fig. 53 C); and *fibrous connective tissue*, in which the intercellular material is composed of fibers, is distributed widely as a binding tissue in many organs. The intercellular fibers of fibrous connective tissue are of two kinds, collagenous and elastic. The *collagenous* or *white fibers* are very fine and occur in bundles, whereas *elastic* or *yellow fibers* are thicker and occur singly. Fibrous connective tissue in which both collagenous and elastic fibers occur is found in the submucosa of the digestive tract and in the dermis of the skin (Fig. 53 D). Fibrous connective tissue in which collagenous fibers predominate is found in tendons, and that containing chiefly elastic fibers is found in the walls of larger arteries and in certain ligaments (Fig. 53 E). The

cells of fibrous connective tissues are spindle-shaped or irregular in outline and possess relatively little cytoplasm.

The second subclass of sustentative tissues is *cartilage*, which is a supporting tissue. The intercellular material in cartilage is sometimes

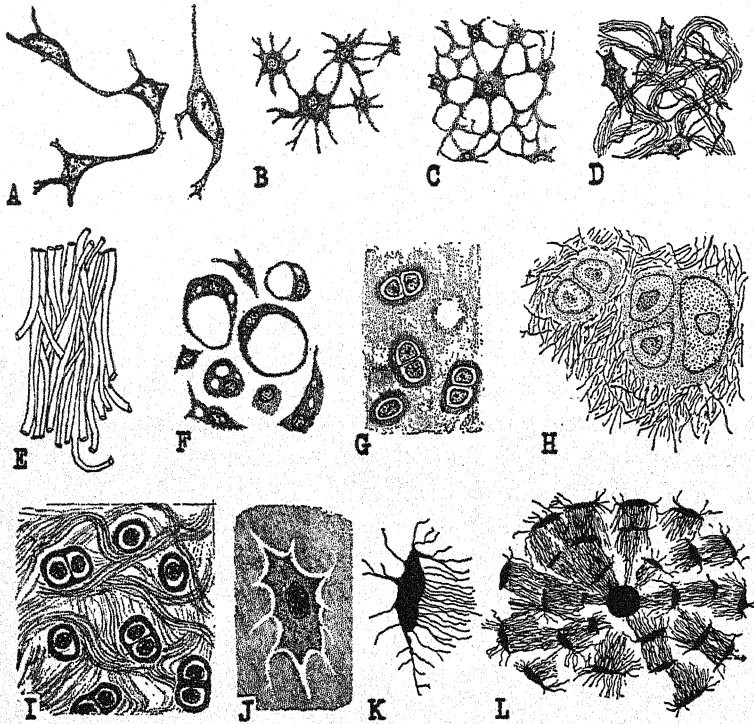


FIG. 53. Sustentative tissues. *A*, cells of mucous connective tissue, which occurs in the umbilical cords of mammals; the gelatinous intercellular material is not represented. *B*, mesenchyme cells. *C*, reticular connective tissue from the spleen. *D*, fibrous connective tissue from the submucosa, showing both collagenous and elastic fibers. *E*, elastic fibers of fibrous connective tissue from the nuchal ligament of the ox; no cells are shown. *F*, adipose tissue, showing various stages of storage of fat drops in the cells. *G*, hyaline cartilage from the end of a rib, showing cells and an empty lacuna. *H*, elastic cartilage from the external ear, showing capsules of hyaline cartilage and elastic fibers. *I*, fibrous cartilage from an intervertebral disk, showing capsules of hyaline cartilage and collagenous fibers. *J*, bone cell lying in a lacuna. *K*, bone lacuna and canaliculi from dried bone. *L*, Haversian system in which lacunæ are arranged concentrically around a central or Haversian canal; canaliculi connect the lacunæ and the canal.

(*A*, *E*, *H*, *K*, and *L* from drawings by D. F. Robertson.)

hardened by impregnation with inorganic salts, chiefly those of calcium. Here the cells are more or less rounded and lie in spaces known as *lacunæ*. When the *matrix* between the cells is translucent and apparently structureless, the tissue is called *hyaline cartilage* or gristle (Fig. 53 G). Hyaline cartilage is found at the ends of long bones, at the ends of ribs, and in the cartilages of the nose and trachea. The cartilage of the external ear contains elastic fibers in its matrix and, therefore, is known as *elastic cartilage* (Fig. 53 H); that found between the vertebræ has collagenous fibers in its matrix and is called *fibrous cartilage* (Fig. 53 I).

Bone, or osseous tissue, is characterized by its very hard matrix, which is impregnated with calcium and phosphorus salts. There is twice as much inorganic material in bone as there is organic. The long bones of the body, such as the femur, have a central marrow cavity filled with yellow or fatty bone marrow. In the much smaller marrow spaces at the ends of long bones and in the vertebræ and sternum is found the *red bone marrow*, which is the site of differentiation of red blood cells and of granular white blood cells. Bone marrow is not osseous tissue; it is merely contained in the cavities of bones. The bone cells lie in *lacunæ* within the matrix (Fig. 53 J and K). A very typical arrangement is that of the *Haversian system*. This consists of a central Haversian canal which contains an artery, a vein, and a nerve, surrounded by concentrically arranged rows of *lacunæ* in communication with one another and with the central canal by means of minute spaces, the *canaliculi* (Fig. 53 L). Lymph circulates in these canaliculi and furnishes a passageway for foods and wastes between blood and cells.

In *adipose tissue* there is no intercellular material, and the stellate mesenchyme cells become transformed into rounded cells which serve to store fat (Fig. 53 F). In fully differentiated adipose cells a large drop of fat is surrounded by a film of cytoplasm, which contains the nucleus. The large drop of fat is formed by the coalescence of numerous finer drops that are deposited in the cytoplasm during the specialization of fat-storing cells.

Vascular Tissue. The vascular or circulating tissues are the blood and lymph and are characterized by a liquid intercellular material, the *plasma*. In *blood*, two kinds of cells are suspended in the plasma. Of these the *red blood cells*, or *erythrocytes*, contain the iron-bearing hemoglobin in combination with which oxygen is carried in the blood (Fig. 54 A and B). The average human being has about 6 liters of blood, and each cubic millimeter of it contains $4\frac{1}{2}$ to 5 million red blood cells. In mammals the red cells lose their nuclei during their

differentiation, are consequently very short-lived, and must be replaced constantly. Red blood cells are differentiated in the red bone marrow in adults, and, if they are not formed in adequate numbers, the individual becomes anemic. The red cells are destroyed by macrophages (*cf.* p. 44) located along the walls of the capillaries of the spleen and liver.

White blood cells are frequently irregular in shape, since they are capable of amoeboid movement and migrate through the walls of capillaries and among the cells of other tissues (*cf.* p. 44). Wandering

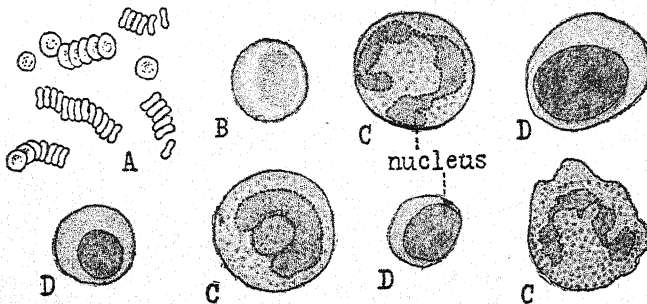


FIG. 54. Vascular tissue. A, mammalian erythrocytes arranged in rouleaux. B, single mammalian erythrocyte (non-nucleated). C, granular leucocytes with polymorphic nuclei; one with irregular cytosome. D, non-granular leucocytes or lymphocytes.

white blood cells can ingest solid particles like bacteria and other foreign bodies into their cytosomes and function in this way in the event of infections or wounds in any part of the body. These white blood cells are known as microphages. Macrophages of the connective tissue are the chief local defenders in what is known as the inflammatory reaction, or first line of bodily defense, at the site of an infection. There are only about 8 to 10 thousand leucocytes in a cubic millimeter of blood in a healthy individual, but the number may be greatly increased in illness. Blood counts are effective aids in the diagnosis of disease. Two main classes of white blood cells are distinguished, those in which the cytoplasm does not contain granules and those in which the cytoplasm is granular. The most abundant kind of non-granular leucocyte is the *lymphocyte* (Fig. 54 D), which is about the size of an erythrocyte and is differentiated in the lymph nodes and in the spleen. Another much less frequent and larger non-granular leucocyte is the *monocyte*. Granular leucocytes, all of which are larger than the other blood cells, have nuclei conspicuously irregular in shape and are called *polymorphonuclear leucocytes*

(Fig. 54 C). There are three kinds, distinguished by the staining reactions of the cytoplasmic granules. Granular leucocytes differentiate in the red bone marrow.

Slightly more than half the volume of the blood is normally plasma, which is the carrier for all substances, except the oxygen, transported by the blood. Plasma contains, in addition to the blood cells, the blood *platelets*, which appear to be fragments of cytoplasm of uncertain origin and function. It also contains many submicroscopic constituents which are very important. One of these is a protein known as *fibrinogen*, which becomes changed to *fibrin*, in the meshes of which the cells are held when blood clots. The clotting of blood acts to seal damaged blood vessels and prevent further loss of blood. Blood does not clot unless a vessel is ruptured, unless there is tissue damage. In circulating blood there is a substance known as *prothrombin*, the formation of which depends on the presence of vitamin K (cf. p. 21). In the presence of calcium salts prothrombin is transformed into *thrombin*, which, in turn, conditions the change of fibrinogen to fibrin. This reaction does not occur in a closed blood vessel because of a substance called *heparin*, or *antithrombin*. When a vessel is broken, the damaged tissue cells and also disintegrating platelets release a substance known as *thromboplastin*, or *thrombokinase*, which neutralizes the effect of heparin. Then thrombin is formed from prothrombin, and, in turn, fibrin is formed from fibrinogen; a clot occurs. When drawn blood clots in a bowl and is allowed to stand, the clot contracts, and a pale yellowish fluid is squeezed out. This fluid is what remains of the original plasma. It is called blood *serum* and contains, among other things, the substances which immunize against certain diseases.

One of the most important functions of the blood is the transportation of oxygen in combination with the hemoglobin of the red blood cells. Death quickly results from loss of blood in warm-blooded animals because oxygen is no longer delivered to the cells of the body in adequate amounts. In medical practice a blood transfusion may save a life after hemorrhage or in severe anemia. When transfusion was first attempted, it was often found that the patient died as soon as blood from another person was introduced into his vessels. The reason is that the red cells of the donor blood clump or stick together; they are agglutinated as a result of a reaction between proteins of the plasma and proteins of the red cells. These clumps prevent the free flow of blood in the capillaries and thus cause death. About 1900 it was discovered that the blood of any human being falls into one of four types, depending on the presence in the red cells of either substance A or B, of both A and B (AB), or of neither A or B (O).

About 45 per cent of the human race have blood of type O; 42 per cent, type A; 10 per cent, type B; and 3 per cent, type AB.

The substances A and B are examples of what are called *antigens*. The substances in the plasma which react with A and B to bring about agglutination are examples of *antibodies*. They are what are known as normal antigens and antibodies. In an individual whose red cells contain antigen A the antibody for A does not occur; such individuals will carry antibodies for B. If blood of type B or O, both of which contain antibodies for A, is placed in the vessels of a type A individual, agglutination will occur.

Proteins, such as bacteria, which are foreign to a particular species of animal and which invade its tissues are also known as antigens. The tissues of the animal react to the presence of the foreign protein by producing antibodies that combat the effects of the antigen. Such antibodies are called immune antibodies and become abundant in the blood plasma, where they remain for varying lengths of time and provide immunity to reinvasion by the foreign protein or antigen that conditioned their production. Thus, permanent or transitory *active acquired immunity* results from having recovered from some disease.

The capacity of animals to synthesize substances protective against foreign proteins can be utilized to protect human beings against diseases. If minute quantities of the pathogenic material are introduced into the body, its tissues will produce abundant antibodies, even though the amount of infective material gives only transitory symptoms of the disease. Thereafter, these antibodies are responsible for an *artificial acquired immunity* to the disease in question; this immunity may be permanent or may have to be renewed at intervals. Dead bacteria are used for inoculation against typhoid and paratyphoid, viruses of reduced virulence are used in vaccination against smallpox or inoculation against rabies, and the toxins; or poisonous substances, produced by the bacteria are injected in inoculation against diphtheria.

Antibodies produced in other animals can be used to give *passive immunity*, usually of short duration, or to combat antigens in human beings in the control of disease. Thus, antibodies, also called antitoxins, against the toxin giving symptoms of diphtheria are produced by horses inoculated with the toxins produced by the diphtheria bacilli and can be obtained in the serum which separates when the horse's blood clots after being drawn. Such *immune serum* administered to an individual enables him to combat effectively the toxin or poison produced by the diphtheria bacillus before antibodies are produced in adequate quantities in his own tissues. After a wound is

received under circumstances where tetanus bacilli might be present, tetanus antitoxin, also from horses, is routinely administered, in order to protect against the toxins these bacilli would produce. Soldiers in World War II were given inoculations of tetanus toxin and antitoxin in order that they might acquire artificial immunity against this rapidly fatal bacterium.

It may be noted here that some individuals have what is called *natural immunity* to certain diseases. This immunity may be the result of inheritance of a capacity to form certain antibodies, such as the natural antibodies against antigens A and B of the red blood cells. Very slight and unnoticed infection with the causal agent of the disease may also bring about what seems to be natural immunity.

Immunity and resistance to disease must not be confused. Immunity is protection against a specific pathogenic agent. Resistance is non-specific and may depend on many factors.

The quantity of blood in the circulatory system is important in connection with the ease of its circulation and the adequacy of supply to all regions. When blood is lost in amounts insufficient to cause death from oxygen want, a condition known as shock may result. This condition can be controlled by increasing the blood volume through the addition of plasma without the red cells. Typing is not necessary for such transfusions. In World War II one of the greatest contributions of science to the saving of human life was the development of methods of separating the plasma from the great quantities of blood donated by non-combatants, preventing it from clotting, and drying it in such a way that it would keep indefinitely. The dried powder was sent to all fronts along with triple-distilled water, with which it was mixed before use in combating shock in wounded men.

Lymph differs from blood in that it does not contain erythrocytes and granular leucocytes. The plasma of lymph is derived from the blood by filtration through the walls of the capillaries and does not contain all the constituents of blood plasma. The importance of lymph as the pathway between blood and the cells of the body should be recalled.

Contractile Tissue. Contractile tissues, known as muscle cells, are of three kinds: non-striated, cardiac, and striated. The cytoplasm of muscle cells is characterized by the presence of numerous fine fibers, which are placed longitudinally. The shortening and thickening of these *muscle fibrillæ* result in the contraction of the individual cell and are therefore responsible for the particular function of this kind of tissue, the production of motion. *Non-striated muscle* cells are typically spindle-shaped with the nucleus centrally placed (Fig. 55 A

and B). These cells usually occur in sheets loosely held together by fibrous connective tissue. This kind of muscle is found in the wall of the digestive tract, in the urinary bladder, and in the walls of blood vessels and is sometimes called involuntary muscle because it is not under conscious nervous control.

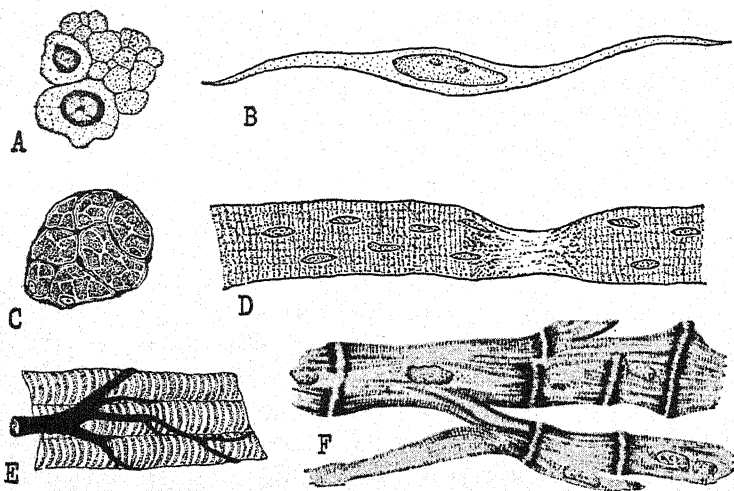


FIG. 55. Contractile tissues. A, non-striated muscle cells in cross-section; note that the cytosomes of many of the cells are not cut through in the region of the nucleus. B, isolated non-striated muscle cell from the wall of the digestive tract, showing spindle-shaped cytosome and single nucleus. C, cross-section of a voluntary muscle; the striated muscle cells are held together in bundles by fibrous connective tissue. D, portion of a striated muscle cell, showing its multinucleate condition and the cross-striations; the cell has been injured near its right end in order to show the cell membrane. E, striated muscle cells, showing blood supply. F, cardiac muscle cells from the human heart.

(A, B, C, and E from drawings by D. F. Robertson; F, from E. A. S. Schäfer, "Essentials of histology," copyright, 1916, by Longmans, Green and Co., reprinted by permission.)

Cardiac muscle is found only in the heart and is capable of rhythmic contractions (Fig. 55 F). The cells are arranged in the form of a syncytium; that is, the cylindrical cytoplasmic units containing the nuclei are not separated from one another by membranes where they meet at their ends. These units branch and unite in such a way that a network is formed. The fibrillæ of cardiac muscle are made up of regions of different density so that the cytoplasm presents an irregularly striated appearance.

Striated muscle is known sometimes as skeletal muscle because it is attached to the bones and by its contractions produces motion of body parts which are supported by bones (Fig. 55 D and E). Since these muscles can be coördinated consciously, they are also called voluntary muscles. They appear striated because the fibrillæ have regions of different density, which occur at such regular intervals as to give a distinct cross-striated appearance to the cytoplasm. The cells are cylindrical, sometimes very long, and each contains many nuclei; that is, the cells are multinucleate. Fibrous connective tissue serves to bind together striated muscle cells and forms sheaths that enclose great numbers of these cells which make up the visible muscles, such as the gastrocnemius or the biceps (Fig. 55 C). These connective tissue sheaths are continuous with the tendons by means of which muscles are attached to bones.

Nervous Tissue. The cells of nervous tissue are differentiated in such a way that they are capable of receiving stimuli in some regions, of transmitting nervous impulses from one part of the body to another, and of discharging these impulses. The general functions of nervous tissue can, therefore, be stated as reception, transmission, and discharge. These activities condition the coördination of the organism as a whole. In the vertebrates the capacity to receive stimuli has been lost by all but a few nerve cells. Most of the nerve cells in vertebrates are capable only of transmission and discharge of nervous impulses. A nerve cell, or *neuron*, is composed of a nucleus surrounded by a relatively small cytosome, which is prolonged into two or more processes of varying lengths, having nerve fibers of two types. Some taper along their lengths and have branches which come off at varying angles; these are called *dendrites*. Others are seen to be of uniform, small diameter, with branches at right angles to the main fiber, and surrounded by a myelin sheath containing compound lipids (Fig. 56 E); these are the *axons*. Typically, impulses are transmitted toward the nerve-cell body over the dendrites and leave the cytosome over axons. Where there are only two cytoplasmic extensions, or nerve fibers, the cell is called a *bipolar neuron* (Fig. 56 A and B). Cells with more than two fibers are known as *multipolar neurons* (Fig. 56 C). Such cells never have more than one axon. The cell bodies of neurons are sometimes found in groups, or *ganglia*, outside the central nervous system; other nerve cell bodies occur in the gray matter of the central nervous system. When nerve fibers are bound together and surrounded by fibrous connective tissue, they form the visible *nerves* of the peripheral nervous system (Fig. 56 D); nerve fibers also make up the

white matter of the central nervous system. A nerve fiber is always continuous with the cytosome of a neuron. As will be recalled, neurons are named according to their positions in a reflex arc, but these names do not indicate subdivisions of nervous tissue (*cf.* pp. 70-71).

Organs. The tissues that have been described illustrate the various types of specialization that cells undergo in the vertebrate body. Particular tissues are capable of performing their special functions alone,

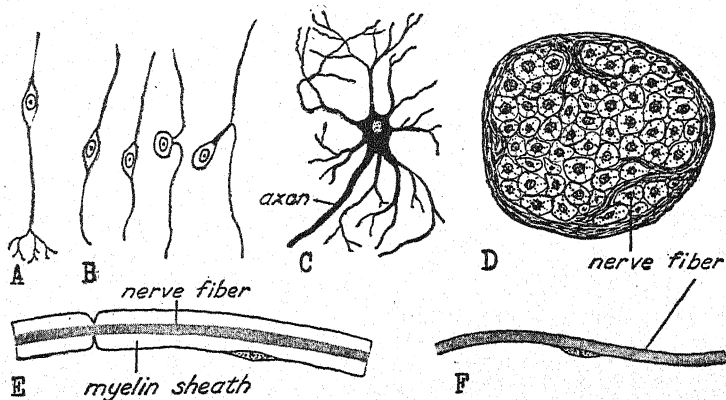


FIG. 56. Nervous tissue. *A*, typical bipolar neuron from the olfactory epithelium. *B*, transformation of a bipolar neuron into the type found in the dorsal root ganglia of spinal nerves. *C*, multipolar neuron, showing cytosome with numerous dendrites and a single axon. *D*, bundle of myelinated nerve fibers surrounded by fibrous connective tissue, as in the spinal and cranial nerves; each nerve fiber is surrounded by a myelin sheath. *E*, portion of a single myelinated nerve fiber; the interruption in the myelin sheath is called a node of Ranvier; a nucleus is seen in the neurilemma, or outer membrane. *F*, portion of an unmyelinated nerve fiber, characteristic of autonomic nerves; a nucleus of the neurilemma is shown.

but they usually occur grouped in organs. Thus, *organs* are groups of tissues associated for the performance of a special function. For example, if the wall of the small intestine of a mammal is examined microscopically, it is found to consist of layers known as the *peritoneum*, the *longitudinal* and *circular muscle layers*, the *submucosa*, and the *mucous membrane* (Fig. 57). The peritoneum consists of simple squamous epithelium and functions as a covering membrane. Both longitudinal and circular muscle layers are of non-striated contractile tissue, bound together by fibrous connective tissue, and their contractions produce the muscular movements that mix the food contents of the small intestine and push them along toward the large intestine

(cf. Fig. 16, p. 32). Fibrous connective tissue, containing both collagenous and elastic fibers, is the distinguishing tissue of the submucosa and serves to support the numerous vessels carrying blood and lymph. This layer also provides the elasticity essential for the expansion of the intestinal lumen, in addition to carrying the circulatory fluids necessary for absorption. The mucous membrane, functioning in secretion and absorption, is composed of simple columnar epithelium, which forms the lining of the tract; a layer of reticular connec-

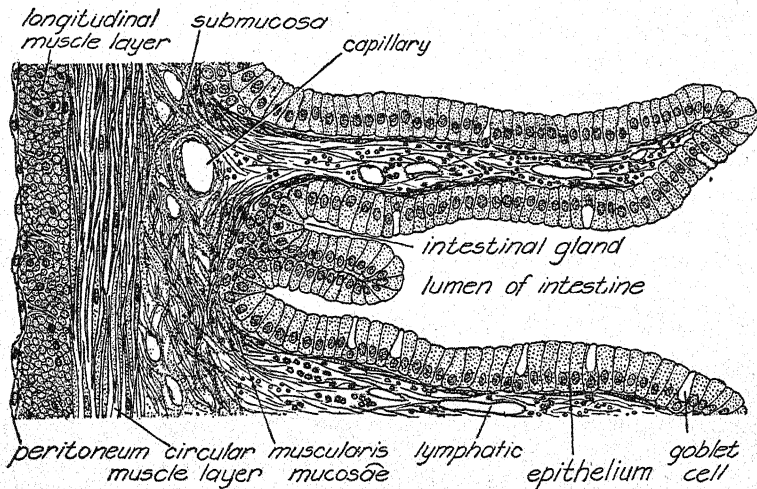


FIG. 57. The wall of the small intestine of an amphibian, in section; semi-diagrammatic.

tive tissue (lamina propria), which forms the cores of the villi; and a thin layer of non-striated muscle cells (muscularis mucosæ), which is the outermost layer lying adjacent to the submucosa. These several tissues are associated to form the small intestine, in which digestion and absorption occur, and each tissue contributes its part of the function of the whole organ. In addition to the grouping of cells to form tissues and of tissues to form organs, organs are associated to form the systems described in the discussions of morphology and physiology.

Summary. An understanding of the vertebrate body as a whole is to be gained in terms of the cells which are the units of both structure and function. Let us consider briefly, for the purpose of illustrating this statement, some of the activities of a common vertebrate, such as a frog. The structure of such an animal is familiar, and the general relations of parts and their functions are well understood. If we imag-

ine a frog that has not fed recently to be sitting on the bank of a stream, we know that as a result of dissimilation and the consequent using up of protoplasmic constituents it will be necessary for the animal to obtain food. If an insect comes within the frog's range of vision, the cells of the frog's retina receive the stimulus produced by the appearance of the insect. Within these retinal cells nervous impulses are set up which pass along nerve-cell processes toward the brain (*cf.* Fig. 44, p. 83). In the visual centers of the brain the impulses are transmitted to other cells of the nervous system and eventually go out along nerve fibers leading to the muscle cells of the frog's tongue. The effect produced is the contraction of certain muscle cells, resulting in the movement of the tongue for the capture of the prey.

The contact of the insect with the lining of the frog's mouth produces closing of the mouth, which in turn stimulates the act of swallowing. These activities, of course, result from muscle-cell reactions. In the stomach and intestine the insect is digested by the enzymes of the digestive juices secreted by the gland cells in the wall of the tract and in the pancreas and liver. These enzymes are secreted at the proper time because of the coördinating mechanism of nerve cells and their processes, or because of the production of endocrines by certain cells and their effects upon other cells (*cf.* p. 56). After digestion and absorption have occurred, the simple foods are carried in the blood plasma to capillary networks and pass out through the walls of the capillaries to the many different kinds of cells that compose the organs of the body. In the protoplasm of cells throughout the animal, assimilation occurs. During its stay out of the water the frog is carrying on respiratory movements of the nostrils, the floor of the mouth cavity, the glottis, and the body wall. These movements are produced by the activities of muscle cells and coördinated as a result of nerve-cell reactions which are dependent, in turn, upon the production of carbon dioxide by cells in all regions of the organism. Oxygen, forced into the lungs by these respiratory movements, passes through the walls of the lungs into the blood, where it enters the red corpuscles and combines with hemoglobin. In capillaries throughout the body, oxygen leaves the red cells and the blood stream to enter the protoplasm of all types of cells, where it takes part in the oxidative reactions of metabolism. As a result of dissimilation, excretions are produced, reach the blood by diffusion, and are eliminated from the body through cells in the lungs, skin, liver, and kidneys. A continuation of this discussion would only add further examples of the same kind. Thus, we see that the general activities of animals are to be explained

in terms of simple cell and tissue reactions, built up into complex activities as a result of coördination.

Cell Division

When cells were first discovered, it was thought that they arose spontaneously by a sort of crystallization. The nucleus was interpreted by some early investigators as a new cell in the process of formation. As the microscope was perfected and more observations were made, new cells were found to be formed as the result of the division of previously existing cells, and in no other way. Periods of division alternate with periods during which the cell is said to be in the vegetative or nutritive stage, that is, when it is either growing or maintaining itself as a functional unit of the organism (Fig. 61). The cell is sometimes referred to, at this time, as a resting cell, but no designation could less adequately describe it during this period of metabolic activity. After a cell has reached a certain size, it may divide. Whether or not cell size is the only factor conditioning cell division, it is certainly a very important one. The division of the cytosome is always preceded by division of the nucleus, which may occur by the method of amitosis or by mitosis.

Amitosis. In *amitosis*, or direct nuclear division, the nucleus becomes somewhat elongated and constricts into two parts which are about equal in volume. The nuclei of certain types of cells may divide amitotically without division of their cytosomes and thus give rise to multinucleate cells. However, the cytosome may divide after the nucleus is constricted, and two new cells are formed. The distribution of nuclear components is only approximately equal in this direct process of division. Such a type of division apparently occurs most often in cells that are very specialized, very old, or in some abnormal or degenerating condition.

Mitosis. *Mitosis* is the typical method of nuclear division. It is called the indirect method because it involves changes that are more complicated than the simple constriction of amitosis. The process of mitosis, which was first fully studied in animal cells by Walter Flemming in 1878, is divided for purposes of description into four continuous stages: the prophase, the metaphase, the anaphase, and the telophase.

The general structure of a vegetative cell should be recalled with particular reference to the centrosphere and centrioles and the delicate chromatin threads of the nucleus (*cf.* p. 92). In some cells there are two centrioles during the vegetative phase; in others, only one. For

this account, let us consider a cell in which two centrioles are present. Among the earliest changes to occur in the *prophase* of mitosis is the separation of the two centrioles toward opposite sides of the nucleus (Fig. 58). At the same time the region of the centrosphere appears to be filled with fine striations, as if fibers were present. The fibers

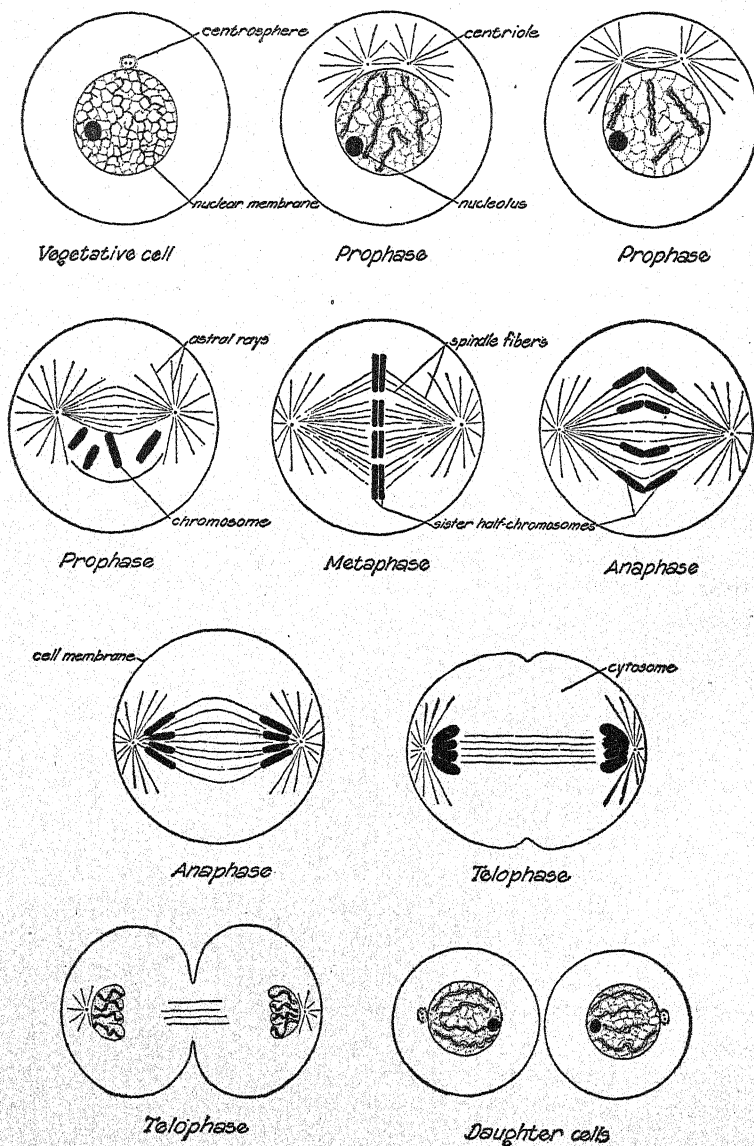


FIG. 58. Mitosis and cell division in animal cells; diagrammatic.

that stretch between the centrioles as they move apart are known as the *spindle fibers*, since they converge toward the centrioles in a typical spindle formation. Fibers called *astral rays* extend freely from each centriole into the surrounding cytoplasm. The structure formed by the fibers and the centrioles has three names: *amphiasma*, because of its resemblance to two conventionalized stars; *achromatic figure*, be-

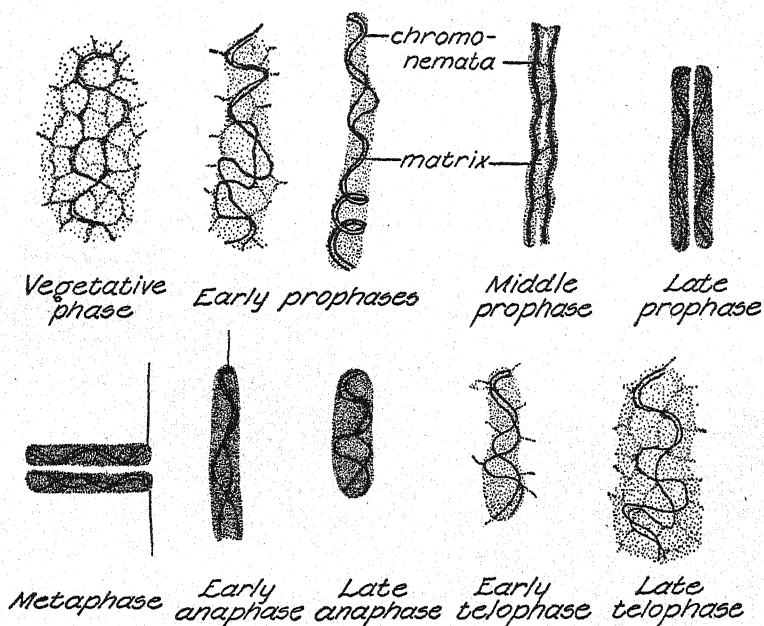


FIG. 59. The chromonemata (black) and matrix (gray) in relation to the behavior of a chromosome during mitosis; diagrammatic. Spindle fibers are shown in the metaphase and early anaphase. The exact stage at which the chromonema is doubled in each half-chromosome is not fully determined:

(Redrawn from L. W. Sharp, 1929, *Botanical Gazette*, vol. 88.)

cause the fibers do not stain; and *mitotic spindle*, because of the arrangement of the fibers that pass from one centriole to the other. The source of the fibers and their exact nature are not clear. While the mitotic spindle is being formed in the cytosome, the delicate chromatin threads are becoming more conspicuous in the nucleus and are seen to be double; that is, two threads are found close together (Fig. 59). Around these two *chromonemata* more of the intensely staining chromatin accumulates and by shortening and thickening forms a *chromosome*. Although careful study of its structure shows that a chromosome contains threads, this would not be suspected ordinarily at the

late prophase, when the staining capacity is very great. A chromosome may be defined as a mass of chromatin, part of which is in the form of threads, the chromonemata.

Chromosomes may be different in size and shape in the cells of an organism; that is, round chromosomes and straight and bent rods occur. The shape of a rodlike chromosome depends on the place of association with a spindle fiber. If the spindle fiber is continuous with the end of a chromosome, it is straight; a subterminal or median association produces a J- or V-shaped chromosome. No matter what the shapes and sizes of the chromosomes are, we find that there are two of each kind as they become fully condensed toward the end of the prophase. Two chromosomes that are alike in shape and size are known as *homologous chromosomes*. The total number of chromosomes visible at the end of the prophase is the *diploid number* characteristic of any species. In any given kind of animal or plant, the same number of pairs of chromosomes will be found in all the cells of the body, with the exception of the mature germ cells (Fig. 60). In some species the males have one less chromosome than the females; that is, one chromosome is unpaired. This same kind of chromosome occurs as a pair in the female. Chromosomes that differ in number in the two sexes are known as *sex chromosomes* (cf. p. 204); the other chromosomes, of which there are two of each kind in both sexes, are called *autosomes*. Coincident with the formation of the mitotic spindle and the condensation of the chromosomes, the nuclear membrane begins to disappear, first in the region next to the spindle, and the nucleolus is lost to view. The chromosomes come into association with the spindle fibers and take up a position midway between the centrioles to form the *equatorial plate* (Fig. 61). Observations on certain kinds of living cells growing in a nutrient medium (tissue culture conditions) indicate that the changes of the prophase take about 8 minutes to occur.

The *metaphase* is the stage at which the longitudinally doubled chromosomes are arranged on the equatorial plate (Fig. 58). The duality that is such a conspicuous characteristic of a metaphase chromosome results from the separation of the matrix after the chromonemata have separated from one another in the middle prophase (Fig. 59). This division of the chromosome in such a way that each half has one-half the chromonemata is of great theoretical significance, since evidence from the study of genetics indicates that the genes, or hereditary determiners, are arranged like beads on a string, that they are located in the chromosomes, and that identical gene-strings are present in all the cells of the body. The mechanism of distribution of

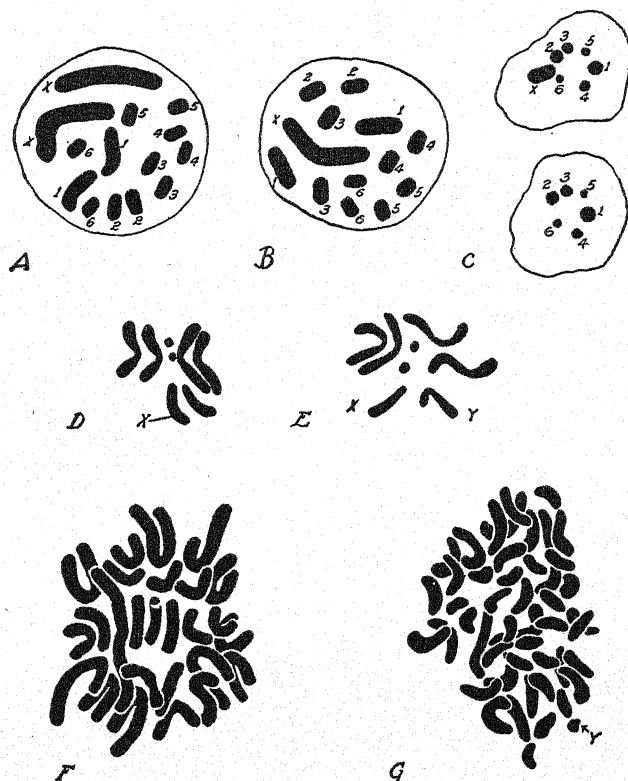


FIG. 60. Chromosomes from various animals. *A* and *B*, an oögonium and a spermatogonium, respectively, of the bug, *Protenor*, showing the two X-chromosomes of the female and the single X-chromosome of the male, as well as the 6 pairs of homologous autosomes; homologous members of the pairs are numbered alike: $\times 2490$. The diploid number of chromosomes in *Protenor* is 14 in the females and 13 in the males. *C*, two spermatids of *Protenor*, one of which has received the X-chromosome at the disjunctional division; each spermatid has one chromosome from each of the pairs of autosomes: $\times 2000$. The haploid number of chromosomes in *Protenor* is 6 in one half of the spermatozoa, 7 in the other half of the spermatozoa and in all of the ova. *D* and *E*, female and male diploid groups from *Drosophila* in which the chromosome number is the same, 8, because the male contains a Y-chromosome: $\times 3800$. *F*, chromosomes of an oögonium of the frog, *R. pipiens*, showing 26 as the diploid number: $\times 2085$. *G*, chromosomes of a human spermatogonium, showing 48 as the diploid number; the Y-chromosome is labeled: $\times 2400$.

(*D* and *E*, modified from C. B. Bridges, 1916, *Genetics*, vol. 1; *F*, from C. L. Parmenter, 1925, *Jour. General Physiology*, vol. 8; *G*, from H. M. Evans and Olive Swezy, 1929, *Mem. Univ. Calif.*, vol. 9.)

chromosomes is, consequently, to be regarded as the mechanism for the distribution of genes. In the chromonema we find a structure which can be regarded as the location of the gene-string, although genes themselves are known to be below the limit of visibility. Each of the sister half-chromosomes in the equatorial or metaphase plate contains a chromonema found in the prophase chromosome.

The beginning of the *anaphase* is indicated by the moving apart of the halves of each chromosome, a moving of one half-chromosome

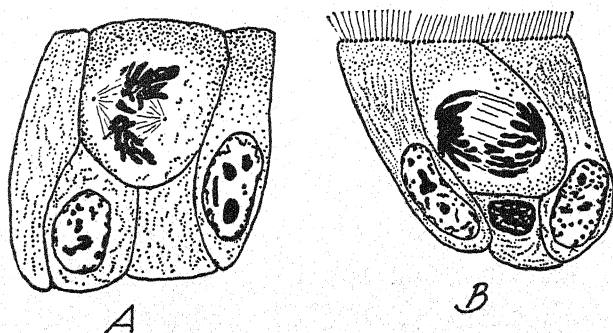


FIG. 61. Cells of ciliated epithelium of a tadpole in stages of mitosis. A, chromosomes at the equatorial plate. B, anaphase. The other cells are in the vegetative phase: $\times 1325$.

(Redrawn from J. E. Kindred, 1927, *Jour. Morphology and Physiology*, vol. 43.)

toward each centriole, or pole of the spindle (Figs. 58 and 61). What produces this movement is still unknown. As the half-chromosomes move toward the poles, careful examination reveals that each contains two chromonemata (Fig. 59). This fact explains why two chromonemata occur in each prophase chromosome; the chromonemata persist from one period of division to the next (Fig. 59).

As the chromosomes near the poles of the spindle, they come to lie very close to one another. This marks the beginning of the *telophase*, during which a new or daughter nucleus is formed from each clump of chromosomes (Fig. 58). A nuclear membrane appears at the periphery of the chromosome group at each pole, and the members of the group begin to separate. However, there is a tendency for the chromosomes to stick together at places along their surfaces, and the effect is net-like. The chromatin progressively loses its capacity to stain, but not uniformly; the threadlike chromonemata stain after the matrix will no longer react with a dye (Fig. 59). Thus, the nucleus of a metabolic cell is formed, and one or more nucleoli soon make their appearance.

The centriole, meanwhile, has divided to form two, and the spindle fibers begin to disappear.

While the telophase of nuclear division is occurring, constriction of the cytosome takes place in the plane of the equatorial plate of the mitotic spindle. When constriction of the cytosome is complete, cell division is finished; the entire process requires somewhat more than 30 minutes for its completion. Two cells have been formed from one by a complicated process of which the most important aspect is the manner of distribution of the half-chromosomes, each containing identical chromonemata. Each new cell gets exactly the same kind and amount of chromatin material. The essential significance of mitosis is the equal qualitative and quantitative distribution of the chromatin.

When the daughter cells enter the metabolic phase, they soon grow to the size typical of their kind. It has been stated that this growth requires from 1 to 2 hours under favorable nutrient conditions. There follows a period of the activity characteristic of the particular kind of cell, and after about 12 hours mitosis may occur again, followed by cytosomal constriction. The times given here are for cells in tissue cultures; other kinds probably differ somewhat, and a variety of bodily conditions doubtless affect division rates. It should be clear that what evidence there is indicates that the chromatin threads found in each anaphase and telophase chromosome persist through the metabolic phase to the succeeding prophase. The importance of this continuity of the essential chromatin material from cell to cell will be increasingly apparent, and the changes that occur during mitosis should be clearly understood.

Differentiation of the Germ Cells

The tissue cells are divisible into groups because of characteristic features of the morphology of their cytosomes. We refer to such cells as specialized, or differentiated, to perform certain functions. The various systems of organs that have been discussed are composed of such cells, which are collectively known as the *somatic cells*, that is, cells making up the body, or soma. There is another type of cell which does not become specialized to perform functions related to either metabolism or irritability. This is the class of *germ cells*, which become differentiated in connection with the capacity of reproduction. In other words, new individuals arise from the germ cells of previously existing individuals.

It has been stated that cells arise by division of previously existing cells, and this statement is true of the germ cells as well as of the

tissue cells. The primitive germ cells arise, of course, from the same ancestor that gives rise to all the somatic cells, that is, from the zygote, the single cell from which the entire organism develops (*cf.* p. 136). In some animals it is possible to trace through successive cell divisions the history of the germ cells, which may be set aside at a very early stage of development (Fig. 62). During the time when the somatic cells are increasing in number and becoming specialized, the primordial germ cells become localized in the reproductive organs in an undiffer-

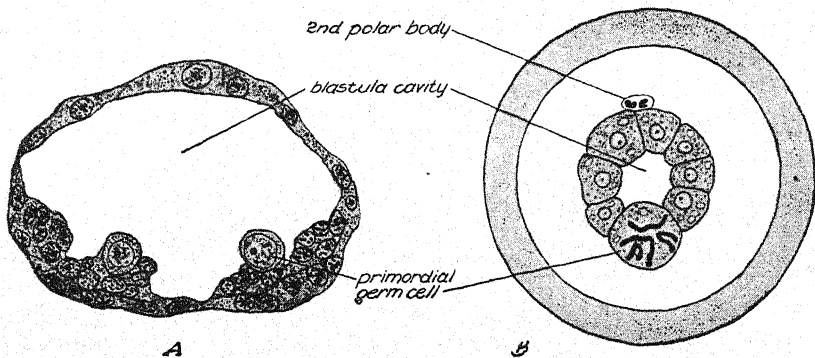


FIG. 62. Origin of primordial germ cells. A, section of a late blastula stage in the development of a mollusk, *Sphaerium striatinum*: $\times 250$. B, section of a blastula stage (32 cells) of a roundworm, *Ascaris equorum* (*A. megalocephala bivalens*): $\times 670$.

(A, from F. H. Woods, 1931, *Jour. Morphology and Physiology*, vol. 51.)

entiated condition. Usually rounded, the cytosome is relatively small in comparison with the nucleus. There is little activity until the animal nears the age of sexual maturity.

Specialization of the germ cells, or *gametes*, occurs in vertebrates during the process of *gametogenesis*, or *maturation*. The maturation or differentiation of a male germ cell is spermatogenesis, the origin of the spermatozoön, or sperm; maturation of a female germ cell is oögenesis, the origin of the ovum, or egg. During gametogenesis the cytosome undergoes modifications that differ in male and female germ cells and that result in the formation of a male gamete which is smaller than the female gamete. Gametes of different sizes are known as *anisogametes* in contrast to the *isogametes* found in some of the unicellular animals (*cf.* p. 255). The nuclear changes in gametogenesis are identical in both types and constitute the process of *meiosis*. In other words, meiosis is the term applied to the distinctive nuclear phenomena that occur during the maturation of the germ cells of verte-

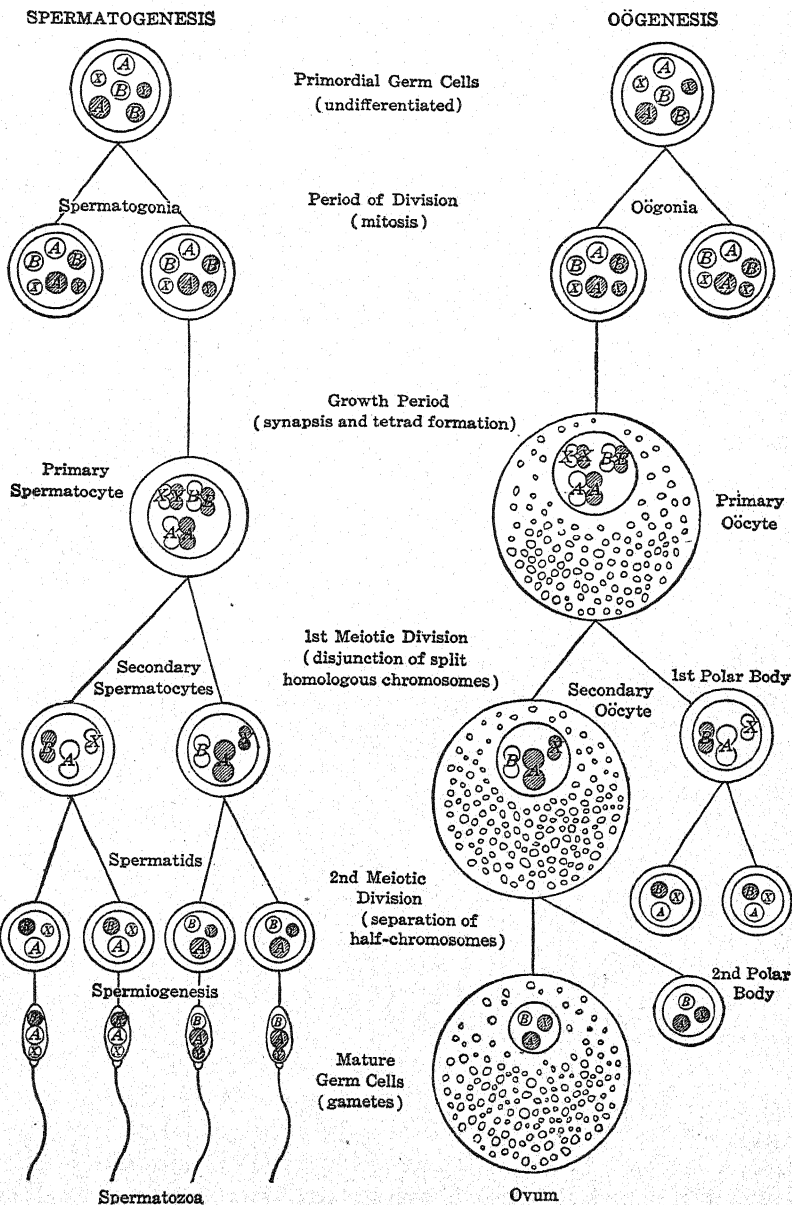


FIG. 63. Gametogenesis in animals; diagrammatic. Homologous chromosomes are lettered alike; A and B are autosomes, X and Y are sex chromosomes. The chromosomes shown in black represent the paternal contribution; the unshaded ones are maternal in origin (*cf.* p. 132). During the growth period food is stored in the cytosome of the primary oöcyte; this yolk remains in the ovum and is not distributed to the polocytes.

brates and other animals. The essential characteristic of meiosis is that it results in the distribution to each mature germ cell of only one chromosome from each of the pairs of homologous chromosomes that are present in the primordial germ cells of an organism. Consequently, each mature germ cell has only half as many chromosomes as the somatic cells and the primordial germ cells had; these chromosomes are unpaired, and the number present constitutes the *haploid number* of the species (Fig. 60). This fact is very significant in the light of the activities of the germ cells and the relation of the chromosomes to the hereditary determiners.

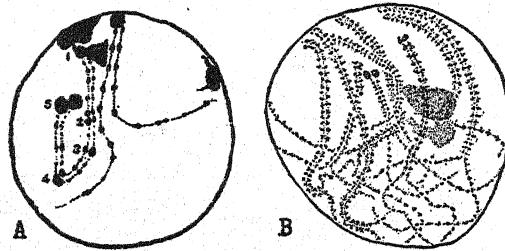


FIG. 64. Nuclei of male germ cells of grasshoppers during the growth period, showing synapsis between homologous chromosomes. In A only two pairs of chromatin threads are shown, and the granules (chromomeres) are numbered to call attention to their structural identity: $\times 1890$. In B many pairing chromatin threads are seen: $\times 1550$.

(From D. H. Wenrich, 1916, *Bulletin Museum Comparative Zoölogy, Harvard College*, vol. 60, and 1917, *Jour. Morphology*, vol. 29.)

If we consider the process of *spermatogenesis*, we find numerous undifferentiated germ cells, known as *spermatogonia*, in the testes (Fig. 63). Spermatogonia give rise to other spermatogonia by the process of mitosis during the *period of division*. When any spermatogonium is ready to begin its differentiation, it enters the *growth period*, during which there is some increase in the size of the cytosome and synapsis occurs in the nucleus. The chromosomes of a spermatogonium occur in pairs of similar size and shape with the exception of the X-chromosome, which either occurs alone or has a companion Y-chromosome, which may not be the same size or shape (Fig. 60). During the growth period homologous chromosomes come to lie side by side in pairs, a phenomenon known as *synapsis* (Fig. 64). The chromosomes at this stage are comparable to the prophase threads of mitosis. As they shorten and thicken, it is seen that each member of a pair is double in a way that is comparable to a metaphase chromosome during mitosis. Thus, each "pair" of chromosomes is really a group

of four half-chromosomes, or *chromatids*, and for that reason is called a *tetrad* (Fig. 66). There are half as many tetrads as there were chromosomes, one tetrad for each pair of homologous chromosomes. The cell is now known as a *primary spermatocyte*. A spindle appears in this cell, and the tetrads become arranged at the equatorial plate. At the anaphase, parts of a tetrad separate in such a way that the two chromatids derived by the division of a single chromosome pass to one pole, while the two chromatids derived by the division of its synaptic mate pass to the opposite pole. This is known as the *first meiotic* or *first maturation division* and is the *disjunctional division* because the two homologous chromosomes which had been paired are now separated, or disjoined, in such a way that they pass to separate cells. The cells arising from the division of the primary spermatocyte are *secondary spermatocytes*; they begin the *second meiotic* or *second maturation division* almost immediately. A spindle is formed, and the divided chromosomes become arranged at the equatorial plate. During the anaphase, separation occurs in such a way that the two chromatids of each chromosome pass to opposite poles of the spindle. This is the *equational division* and is entirely comparable with any mitotic division, except that only half the typical number of chromosomes is present in the cell. The two cells formed by the division of each secondary spermatocyte are the *spermatids* (Fig. 60). Four spermatids arise from each primary spermatocyte, and each one contains one chromatid of the four which are formed by the division of the members of each pair of homologous chromosomes.

Cytosomal differentiation of the spermatids next occurs; this is known as *spermiogenesis* (Fig. 65). The essential changes consist in the outgrowth of a vibratile flagellum, or tail, from one of the centrioles of the spermatid and the loss of most of the cytoplasm. The nucleus becomes very condensed and is surrounded by a very thin layer of cytoplasm in the *head* of the mature *spermatozoön*. The centrioles and a small mass of cytoplasm form the *middle piece*, and the third part is the *tail* by means of which the mature male germ cell, or *microgamete*, is able to swim. The spermatozoön is specialized for motility and contains one-half as many chromosomes as the primordial germ cells and tissue cells contain, one chromosome corresponding to each of their pairs. Four functional spermatozoa are derived from each primary spermatocyte.

The process of *oögenesis*, or maturation of the female germ cell, is entirely comparable to that of spermatogenesis in so far as nuclear changes are concerned; the cytosomal specialization differs (Figs. 63 and 66). The undifferentiated germ cells found in the ovaries are

known as *oögonia* and give rise to other *oögonia* during the *period of division*. Each of these presently enters upon the *period of growth*, and the homologous chromosomes pair in *synapsis* and become divided to form *tetrads*. This is the time when *cytosomal differentiation* occurs in the female germ cell, or *primary oöcyte*, as it is now called. In all female vertebrates, certain of the undifferentiated germ cells form a layer around the primary oöcyte. This envelope, or *follicle*, serves a

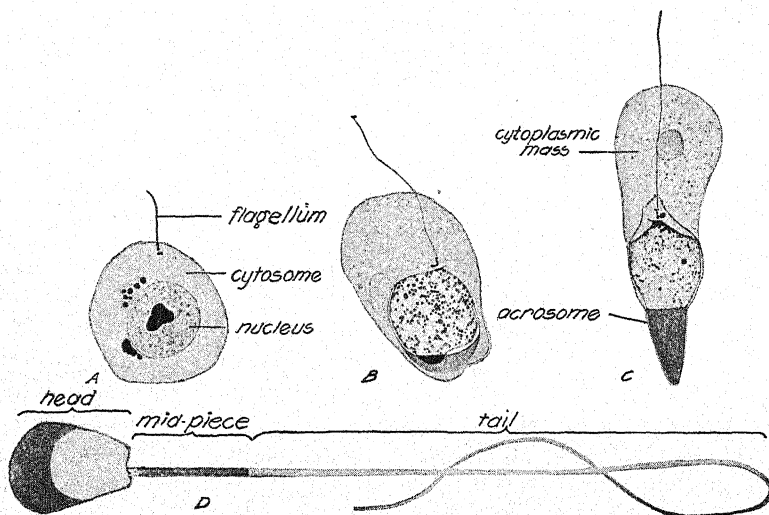


FIG. 65. Stages in spermiogenesis in the guinea-pig. A, spermatid with early growth of flagellum from one centriole. B and C, showing the centrioles near the nucleus, the accumulation of cytoplasm along the flagellum, and the formation of the acrosome, which is the most anterior part of the spermatozoon. D, mature sperm, showing head, mid-piece, and tail; the cytoplasmic mass has been detached and lost.

(From F. Meves, 1898, *Archiv für mikroskopische Anatomie*, vol. 54.)

nutritive function during the storage of food, usually in the form of yolk, which occurs in the oöcyte during the growth period. The follicles of different vertebrates vary in thickness; the follicle of mammals is very large (*cf.* Fig. 69, p. 124). Not all vertebrates store a large supply of food for the young individual that may develop from the egg if it is fertilized. The method and place of development are correlated with the amount of food stored in the female germ cell and will be discussed later (*cf.* p. 136). When food storage is complete, the primary oöcyte divides to form two cells very unequal in size. There is a large cell, the *secondary oöcyte*, containing most of the food, and a very small cell, the *first polar body*, which has only a thin layer of cytoplasm

around its nucleus. The division which produces these cells is the *first meiotic* or *disjunctional division*, and the nucleus in each cell contains half-tetrads, just as does that of each of the secondary spermatocytes. At the *second meiotic* or *equational division* the first polar body divides to form two polocytes, or polar cells, of equal size, but the secondary oöcyte gives rise to a small cell, the *second polar body*, and to the *ovum*, or mature female germ cell, which contains the food that was stored in the primary oöcyte. The three small cells and the ovum have comparable nuclei; each contains one chromosome corre-

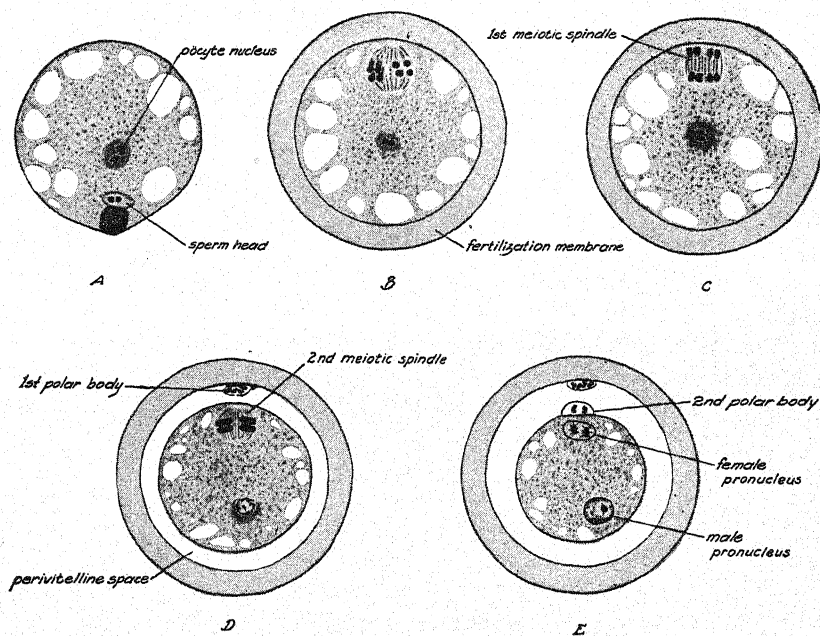


FIG. 66. Meiosis during oögenesis of a roundworm, *Ascaris equorum* (*A. megaloccephala bivalens*). A, a primary oöcyte into which a sperm carrying the haploid number of chromosomes (2) has just penetrated. B, showing 2 tetrads, each containing 4 half-chromosomes (chromatids), on the equatorial plate of the spindle of the first meiotic division. C, showing the anaphase of the first meiotic division with 2 chromatids from each tetrad passing to each end of the spindle. D, showing the 2 pairs of chromatids on the spindle of the second meiotic division. E, showing the nucleus of the mature female germ cell (female pronucleus), the first and second polar bodies, and the nucleus of the sperm head (male pronucleus), which has been inactive since its entrance. The meiotic spindles in *Ascaris* do not have centrioles or astral rays. A perivitelline space is formed between the oöcyte and the fertilization membrane which arises after the sperm enters. All figures $\times 630$.

sponding to each homologous pair in the oögonia and somatic cells. Only one ovum, or *macrogamete*, is produced from each primary oöcyte. The small polar cells are non-functional and die.

All the cells of the vertebrate organism become differentiated in connection with activities of the particular organs of which they form a part. The time of specialization of the germ cells occurs much later in life than differentiation of most of the somatic cells. However, just as differentiation of germ cells continues throughout the period of sexual activity in the organism, differentiation of certain kinds of somatic cells is not confined to the developmental period. Cells wear out or die and are replaced by others recently formed by mitosis from stocks of relatively unspecialized cells. Cells that have not been differentiated are known as *totipotent* or *embryonic cells* because they can give rise to various kinds of cells. The type of cell into which a totipotent cell differentiates depends, apparently, on the location of the cell in the body. Primordial germ cells are totipotent cells. The essential difference between somatic cells and the germ cells is to be referred to their activities: the somatic cells are specialized with respect to the capacities of metabolism and irritability, whereas germ cells are differentiated with respect to the capacity of reproduction. Both groups of cells have the same essential structure of nucleus and cytosome; both are masses of protoplasm and hence have the same requirements for life. Somatic cells contribute to the existence of the germ cells of the same generation, whereas germ cells make possible the existence of somatic cells of the succeeding generation.

CHAPTER 5

REPRODUCTION AND DEVELOPMENT IN CHORDATES

Living organisms are distinguished by the capacities of metabolism, irritability, and reproduction, which are inherent in the protoplasm of all animals. The primary effect of the activities of the organ-systems that are specialized to supply the metabolic requirements of protoplasm and to coördinate the functions of all parts of the organism is to maintain the life of the individual. The individual also exists as a potential parent. As a result of the capacity of reproduction certain parts can become detached and, either alone or after union with protoplasm of another organism of the same kind, can give rise to a new individual capable of becoming like the parent or parents in all essential respects. Reproduction, like metabolism and irritability, is dependent upon a cellular mechanism, and a specialized organ-system is related to this activity of the individual.

The Reproductive System

The reproductive system of vertebrates consists of the *reproductive organs*, or *gonads*, in which the germ cells become differentiated, and the *reproductive ducts*, by way of which the germ cells leave the body. During the development of the individual, the reproductive and urinary systems arise in close association, so that structurally they form what is known as the urino-genital system (*cf.* p. 50). The functions of the two parts of this system are entirely unrelated, and we shall be concerned here with only the reproductive or genital system. In the vertebrates, as in the majority of animals, there are typically two sexes; individuals are either male or female (*cf.* p. 203). Both gonads and ducts differ in the male and female reproductive systems.

In the male frog the two gonads, or *testes*, are suspended by mesenteries, the *mesorchia*, from the dorsal surface of the pleuro-peritoneal cavity ventral to the excretory organs (*cf.* Fig. 2, p. 9, and Fig. 67). This position of the testes in relation to the excretory organs is characteristic of fishes and amphibians, in which the functional excre-

tory organs are mesonephroi (*cf.* p. 50) but are often called kidneys. In reptiles and birds the testes are suspended near the kidneys, but in male mammals the gonads are located posterior to the kidneys and in many species descend until they lie outside the peritoneal cavity in the scrotum. The testis is essentially a mass of small seminiferous tubes, along the walls of which the primordial germ cells are found (*cf.* p. 114). As maturation is completed, numerous spermatozoa fill the cavities

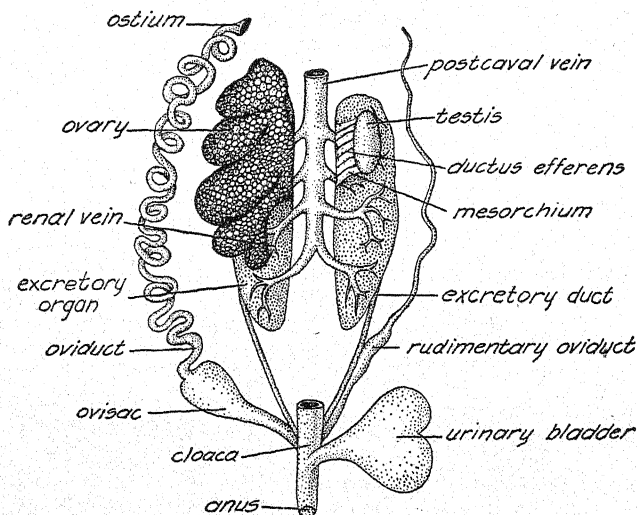


FIG. 67. The urino-genital system of the frog, showing organs of a young female on the left and those of a male on the right.

of the seminiferous tubes, which are continuous with the reproductive ducts. The fishes and frogs have numerous small ducts, the *ductus efferentes* (vasa efferentia), which are continuous with the seminiferous tubules in the testis and also with the excretory tubules. In such animals spermatozoa pass from the tubules of each testis to the ductus efferentes, which are located in the mesorchium, and into the excretory tubules. Thence, the path to the outside is by way of the excretory duct and cloaca, and the male germ cells are shed from the body through the anus. With the replacement of mesonephroi by metanephroi, or true kidneys, a characteristic of reptiles, birds, and mammals, the spermatozoa no longer pass through the kidneys but leave each testis through a coiled duct, the *epididymis*, which is continuous with a *ductus deferens* (vas deferens) that opens into the ventral part of the cloaca in reptiles and birds and into the *urethra*, or neck of the urinary bladder, in mammals (Fig. 68 A).

The female reproductive organs are known as *ovaries*. They are suspended by ovarian mesenteries, the *mesovaria*, ventral to the anterior end of the excretory organs in the frog and vertebrates other than

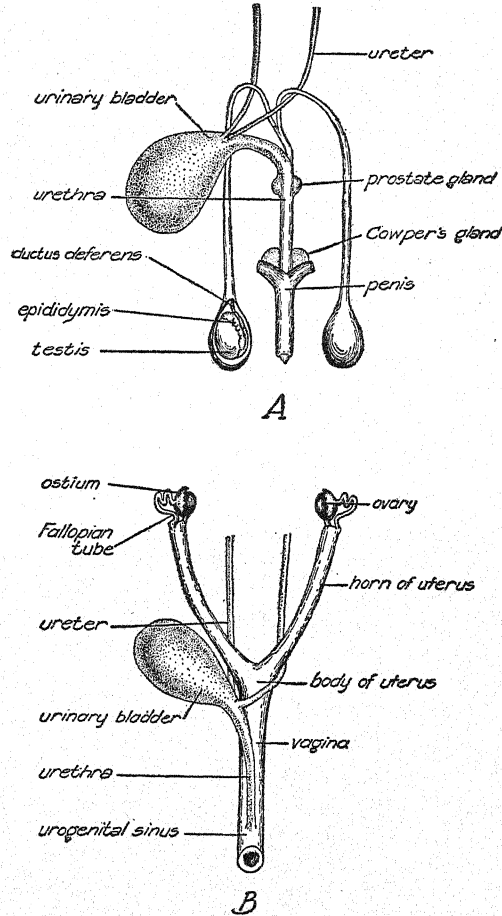


FIG. 68. The reproductive system of the cat. A, in the male. B, in the female.

(Redrawn with modifications from J. Reighard and H. S. Jennings, "Anatomy of the cat," copyright, 1901, by Henry Holt and Co., printed by permission.)

the mammals; a descent of the ovaries into the pelvic region of the peritoneal cavity occurs in such forms (Figs. 67 and 68 B). Ovaries may be saclike, as they are in the frog, or solid, as they are in higher vertebrates (Figs. 70 and 73 A). The wall of an ovary of the frog and the outer layer of an ovary of a mammal are composed, for the

most part, of undifferentiated germ cells which give rise not only to the mature germ cells, or ova, but also to the cells that form envelopes, or *follicles*, around the growing oöcytes (Figs. 70 and 71 and cf. p. 118). In those vertebrates in which the oöcyte stores a large amount of food material, the follicle consists of only two or three layers of cells and becomes very inconspicuous as the growth of the oöcyte is completed. Contrasted with such a condition is the very great growth of the follicle

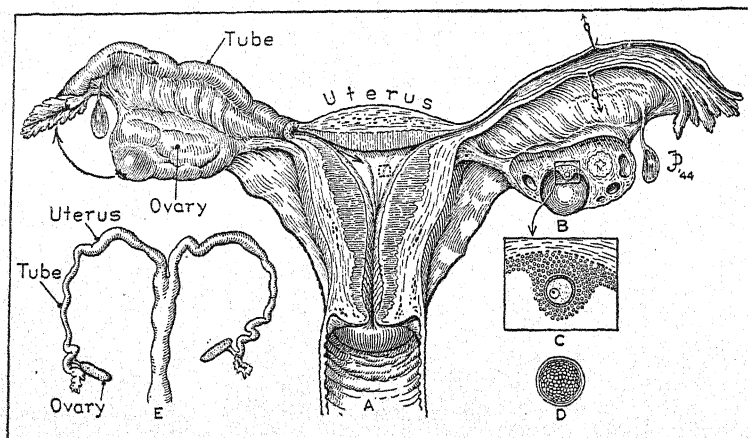


FIG. 69. *A*, diagram of ovaries and reproductive tract in man; the uterus and right Fallopian tube are shown with their walls cut away to reveal the cavities. On the left, arrows indicate the path of the egg from ovary to uterus; this figure is about one-half natural size. *B*, mature follicle with its egg or ovum. *C*, portion of mature follicle surrounding egg. *D*, ovum seen from the outside, $\times 30$. *E*, reproductive tract and ovaries of rabbit; about one-fourth natural size.

(From G. W. Corner, "Ourselves unborn," copyright, 1944, by Yale University Press, reprinted by permission.)

in the mammals in which little food is stored in the oöcyte. The mammalian follicle is vesicular, and its cavity is filled with the follicular fluid, which contains a hormone (cf. p. 60).

The reproductive ducts of the female are the *oviducts*, which are not directly continuous with the ovaries but open into the coelomic cavity. The *ostium*, or opening of the oviduct, is located in the anterior end of the coelom in the frog but lies nearer the ovary in higher vertebrates (Fig. 67 and cf. Fig. 1, p. 8). In many mammals the ostium practically surrounds the ovary (Fig. 68 B). When *ovulation*, or rupture of the follicles, occurs in the frog, the eggs are discharged from the ovary and drop into the coelom, where they are

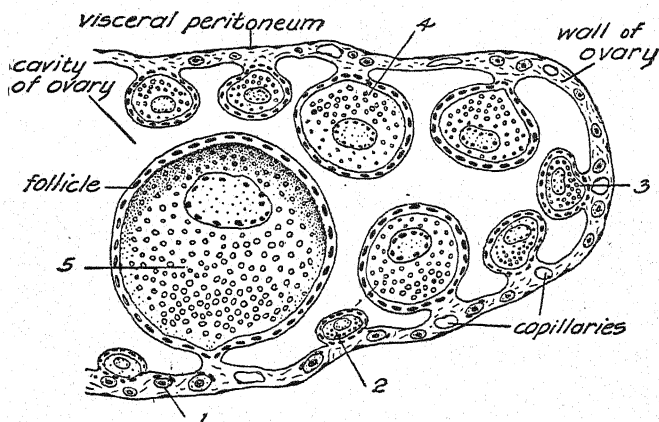


FIG. 70. A lobe of the frog's ovary, in section; diagrammatic. 1-5, successive stages in the growth of the oocytes.

carried through the ostia of the oviducts by the beating of the cilia. In higher forms, the eggs pass directly into the ostia as ovulation occurs and are present in the cœlom only under atypical conditions.

Attention may be called here to the several meanings which the word egg has. We speak of birds' and reptiles' eggs, which most often have been fertilized and are in the process of development, and which contain albuminous envelopes in addition to the female germ cell (Figs. 72 and 73). We refer to ovarian eggs when we mean

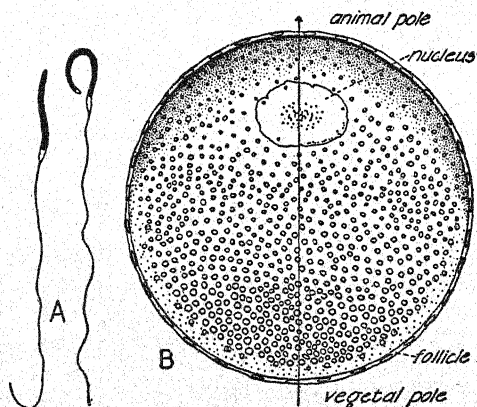


FIG. 71. Germ cells of the frog. A, mature spermatozoa: $\times 1070$. B, an oocyte, with its follicle, at the end of the growth period: $\times 30$; drawn in section to show the unequal distribution of yolk in the animal and vegetal hemispheres and the location of the nucleus in the animal hemisphere; the arrow indicates the egg-axis.

the growing oöcytes, and to tubal eggs when we mean recently ovulated female germ cells which may be either oöcytes or ova (cf. p. 118) or may be fertilized and in the early stages of development. The student should not be confused by the several uses of this word, which are so widely accepted that it would be impossible to change them. Wherever clarity

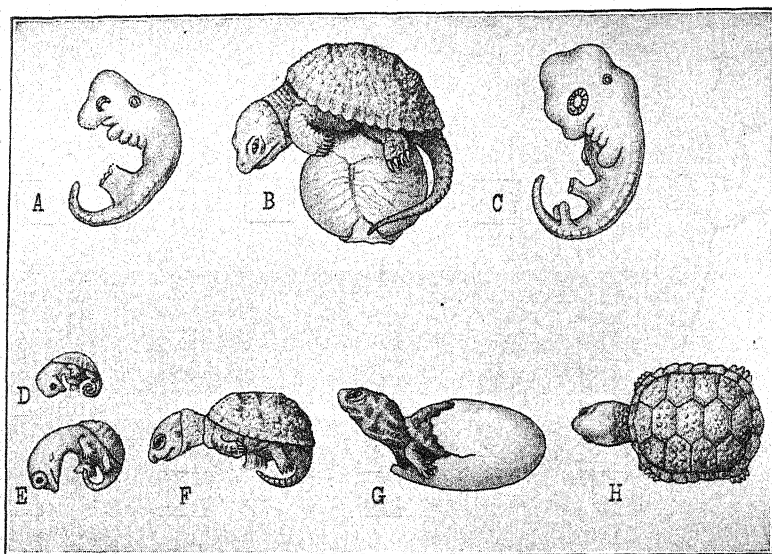


FIG. 72. The development of a tortoise. The eggs, which contain a yolk-laden zygote surrounded by albumen, are laid in a cavity excavated by the female in the ground at some distance from the bank of a pond or stream. Kept warm by the heat of the sun and protected by the leathery coverings of the eggs and several inches of loose soil, the embryos develop until they hatch as miniature adults and immediately return to the water. *A* and *C*, young embryos, dissected from the eggs; gill slits, eyes, ears, regions of the brain, and the cut end of the yolk-stalk can be observed. *D-F*, later embryos, dissected. *B*, embryo like the one shown in *F*, attached to the yolk-sac but removed from the albumen and leathery covering. *G* and *H*, hatching stages.

(Redrawn from L. Agassiz, "Contributions to the natural history of the United States," 1857, Little, Brown and Co.)

demands it, a more restricted term will be used; in other cases the meaning will be clear from the context.

A relatively unspecialized oviduct occurs in the frog. Jelly is secreted by the cells lining the long coiled portion, and the eggs may be stored temporarily in the expanded ovisac which opens into the cloaca, through which the eggs pass to the outside by way of the anus (Fig. 67). The albumen, or so-called white, of a reptile's or bird's

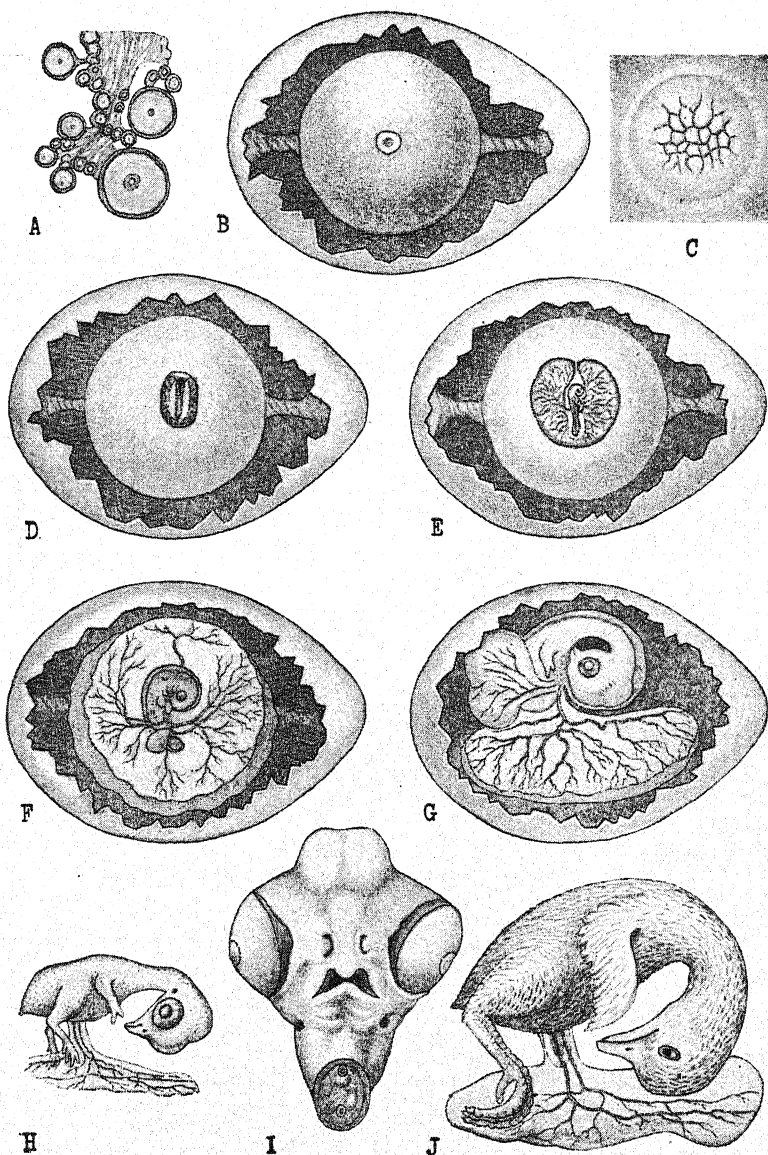


FIG. 73. The development of the hen's egg. *A*, portion of the ovary, showing oöcytes in different stages of growth. *B*, the egg at the time of laying, with part of the shell removed to show the yolkly zygote (the "yolk") suspended by denser cords of albumen (the "white"); the small disk of cytoplasm is shown on the surface of the zygote. *C*, the cytoplasmic disk removed from the egg, to show its cleavage; before cleavage this region is known as the blastodisk and after cleavage it is called the blastoderm. *D-G*, successive stages in the origin of the embryo and the spread of the margin of the blastoderm to form the yolk-sac, in which blood vessels soon appear. The amnion has been formed in *F* and *G* but is difficult to distinguish; in *F* the small sac at the posterior end is the allantois, which is also seen in *G* as the smaller of the two appended sacs. *H* and *J*, later embryos removed from their shells and with the amnion and allantois removed; only the yolk-sac remains in *H*, while the yolk-sac is shown in *J*. *I*, the head of an embryo removed and viewed from the front, showing mouth, sense organs, and remains of the gill furrows.

(Redrawn from M. Duval, "Atlas d'embryologie," 1889.)

egg is secreted by a specialized region of the oviduct, and the egg-envelopes and shell by other regions (Fig. 73 B). Animals that lay eggs which are well supplied with food and in which the young develop outside the body are known as *oviparous*. Among the fishes and reptiles some forms retain the fertilized eggs in a uterine portion of the oviducts during development. In such species the young are nourished by the food stored in the egg, and these forms are referred to as *ovoviviparous*. A few of the most primitive mammals, such as *Ornithorhynchus*, the duckbill (cf. Fig. 462, p. 632), lay eggs and have paired oviducts like those of the reptiles. Other mammals retain the

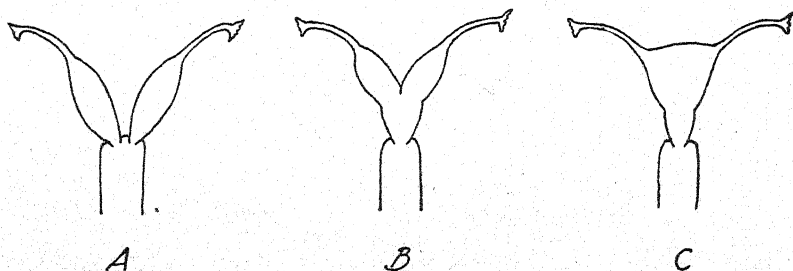


FIG. 74. The oviducts of mammals, showing progressive fusion of uterine portions. A, duplex uterus, as in rabbits; B, bicornuate uterus, as in swine; and C, simplex uterus, as in man.

fertilized eggs during development, and the oviducts exhibit conspicuous modifications related to retention and nourishment of the embryo or developing young individual (Fig. 68 B). These mammals are *viviparous*. The ostial portion of each oviduct is slender and is known as the *Fallopian tube*. Posterior to the Fallopian tube, the oviduct expands to form the *uterus*, which is the region where the embryos develop, and terminates in a short *vagina*, which opens into the urogenital sinus. Although primitive mammals have a pair of oviducts, there is a progressive fusion in higher forms beginning with the vaginal portions, and in man the Fallopian tubes are the only paired parts (Fig. 74).

Vertebrates are typically either male or female, but they pass through a developmental stage in which they are sexually indifferent; that is, it is impossible at such a stage to decide whether the primordial gonads are ovaries or testes, and the primordial reproductive ducts of both sexes are present. During later development the gonads differentiate into either ovaries or testes, and the correlated ducts develop while those of the opposite sex degenerate. In the adult males of some fishes and frogs, however, the oviducts persist as

rudimentary, non-functional organs, vestiges of the indifferent period of development (Fig. 67 and *cf.* p. 668).

Reproduction

Historical. Since Aristotle in the fourth century, B.C., made observations on the developing hen's egg, students have been interested in the origin of new individuals. Before the invention of the microscope the male germ cells could not be seen. Spermatozoa were studied first in 1677 by Antony van Leeuwenhoek, a Dutch microscopist. Several observers soon associated the occurrence of spermatozoa in the seminal fluid with the phenomenon of reproduction, and some workers stated that each spermatozoön contained a fully formed, miniature individual. This tiny individual was called a homunculus and was believed to grow, nourished by the female, until the time of birth (Fig. 75). Such a fantastic idea was opposed by other scientists of the eighteenth century who believed that new individuals were fully formed in the egg cells and that spermatozoa were parasitic in character and entirely unnecessary for reproduction. These ideas of minute individuals encased in spermatozoa or in eggs were responsible for the Theory of Preformation, according to which development was simply the growth of a small individual preformed in the so-called germ.

In 1824 Prévost and Dumas proved that spermatozoa are essential for the formation of new individuals by filtering the seminal fluid of male frogs before mixing it with eggs. No new individuals were formed under such conditions. Even this experiment did not establish the fact that the sperm and the egg united. It was not until 1875 that the actual penetration of an egg by a spermatozoön, followed by the union of the two nuclei, was observed independently by Hermann Fol and Oscar Hertwig in sea-urchins (*cf.* p. 548). When it is recalled that the Cell Theory was formulated in 1838 and 1839 (*cf.* p. 88), the recognition by Hertwig and Fol that the spermatozoön and egg were cells is not surprising. With this recognition a sound interpretation of reproduction, which had baffled students for hundreds of years, was soon reached. The earliest workers had lacked mechanical equipment in the form of microscopes, but the improvement in lenses

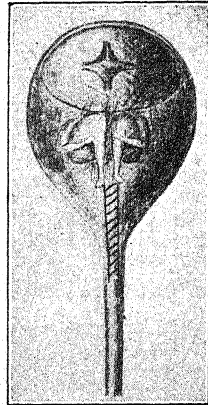


FIG. 75. Homunculus in the head of a spermatozoön.

(From O. Hertwig, after Hartsoeker, 1694.)

was not all that was needed. Progress in science is always dependent on what scientists think about the facts they observe. The conception of cells as the units of structure and function was, and is, as great a scientific tool as the microscope, and we are strikingly impressed with this fact in a study of reproduction and development.

Methods of Reproduction. Reproduction, or the formation of a new individual, is accomplished in several different ways. On the one hand, it may occur without the production of germ cells and be the result of the activity of only one individual—*asexual* or *uniparental reproduction*. On the other hand, germ cells, or *gametes*, may be produced by two individuals and unite in pairs—*sexual* or *biparental reproduction*. Among the unicellular animals asexual reproduction is brought about by *cell division* (cf. p. 291). If this cell division produces two equal cells, it is known as *fission*; if the two cells are unequal in size, the process is called *budding*. Sometimes a process of multiple cell division known as *sporulation* occurs, with the result that many new individuals are produced at the same time (cf. p. 258). Some of the simpler multicellular animals, such as the coelenterates, reproduce asexually by the methods of budding and strobilization; the flatworms undergo fission (cf. pp. 330, 333, 334, and 353). Sexual reproduction occurs throughout the Animal Kingdom by the method of *syngamy*, or union of two gametes to form a *zygote*. When the gametes are differentiated into microgametes and macrogametes, the process of syngamy is known as *fertilization*. Among the protozoans both isogametes and anisogametes occur, but anisogametes are typical of multicellular animals. Syngamy usually takes place in animals that produce anisogametes, but *parthenogenesis*, or development of a macrogamete without union with a microgamete, sometimes occurs, notably among the rotifers and insects (cf. pp. 360, 377, and 520).

Reproduction is typically a function of adult animals; germ cells are produced by mature individuals. However, in one of the amphibians, the axolotl, immature or larval animals give rise to germ cells which function in reproduction. Reproduction by immature animals is called *pedogenesis* and is known to occur in several invertebrate groups (cf. p. 362).

Fertilization. The union of an egg and spermatozoön is known as fertilization, or syngamy, and the resulting cell, which has the capacity to develop into a new individual, is called a zygote. Two separable and very important phenomena, which were recognized almost immediately, are observed during fertilization. In 1875 Hertwig appreciated the fact that it is the union of spermatozoön and egg that stimulates

the egg to begin its development; this aspect of fertilization is known as *activation*. Not until 1883, when Van Beneden studied fertilization in *Ascaris*, was the additional significance of the fusion of cells

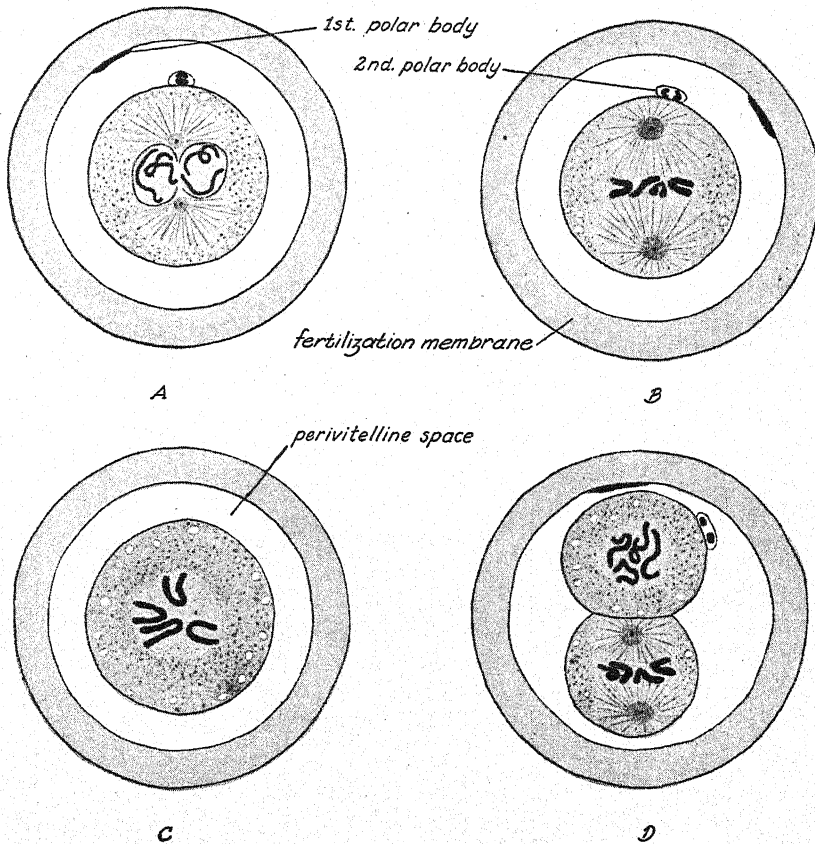


FIG. 76. Amphimixis and early cleavage in *Ascaris equorum* (*A. megalocephala bivalens*), a nematode. A, the male and female pronuclei have approached one another as the mitotic spindle for the first cleavage is formed; each contains the haploid number of chromosomes, which is two. B, the four chromosomes (diploid number) at the equatorial plate of the first mitotic spindle, seen from the side. C, the four chromosomes at the equatorial plate of the first mitotic spindle, seen from one end of the spindle. D, a two-cell stage in which both nuclei are in the late prophase of mitosis (the second cleavage).

All figures $\times 640$.

from two parents recognized. Fol had observed meiosis in 1875, but Van Beneden had much more favorable material and could see that the nuclei of spermatozoön and ovum contributed equally to the

nuclear constituents of the zygote (Fig. 76). The union of the two pronuclei, each containing one chromosome of each of the homologous pairs characteristic of the species, restores the diploid number of chromosomes and is known as *amphimixis* (cf. p. 110). Each zygote, consequently, has the same number of pairs of chromosomes that each

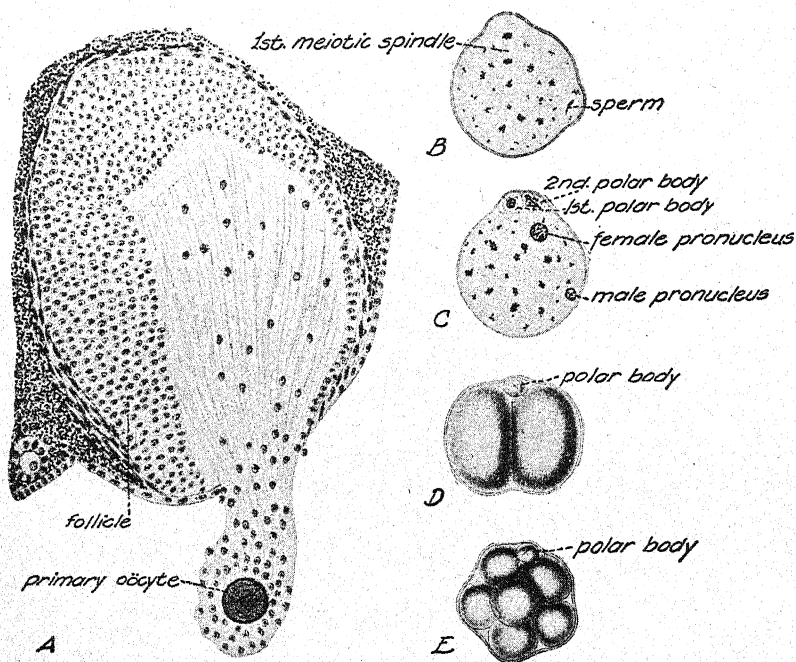


FIG. 77. Reproduction and early development in the mouse. A, ovulation. B, entrance of sperm (activation) and the beginning of meiosis in the primary oocyte. C, meiosis of the egg complete, but before amphimixis. D, two-cell stage. E, eight-cell stage. A, $\times 100$; B-E, $\times 300$.

(From J. Sobotta, 1895, *Archiv für mikroskopische Anatomie*, vol. 45.)

of its parents has, and each parent contributes one chromosome of each pair. Meiosis and amphimixis furnish the physical basis for an understanding of heredity (cf. pp. 176-180).

The process of maturation of the male and female germ cells has been discussed (cf. pp. 113-120). Meiosis and spermiogenesis occur in the seminiferous tubules of the testis, and the spermatozoa are mature when they are shed by the male and penetrate the eggs (cf. Figs. 63 and 65, pp. 115 and 118). The female germ cells are not always mature when the spermatozoa enter. The primary oocytes, surrounded by their follicles, grow and store nutrients in the ovary, and in some

animals both meiotic divisions occur before ovulation; ova are liberated and fertilized. In other animals, the primary oöcyte is ovulated, and the spermatozoön enters before either meiotic division has occurred (cf. Fig. 66, p. 119). Meiosis begins in many vertebrates just before the time of ovulation, and the spermatozoön enters either the primary or secondary oöcyte, which then completes its meiosis (Fig. 77). When it enters an immature egg, the spermatozoön remains quiescent until oögenesis is completed. The nucleus of the spermatozoön, or *male*

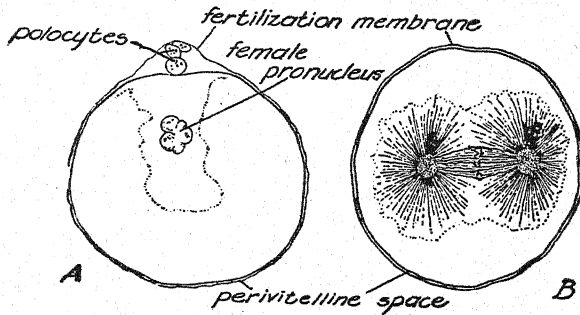


FIG. 78. Early development after artificial parthenogenesis in *Thalassoma*, one of the echiuroids. A, meiosis has occurred within a fertilization membrane, the formation of which was conditioned by a short treatment with dilute acid. B, the first cleavage spindle; only the haploid number of chromosomes is present.

(From G. Lefevre, 1907, Jour. Experimental Zoölogy, vol. 4.)

pronucleus, then becomes rounded and vesicular like the *female pronucleus* before amphimixis takes place.

As long ago as 1785, when Lazaro Spallanzani mixed lemon juice and vinegar, among other things, with frogs' eggs in an attempt to stimulate them to develop, biologists sought to secure activation by artificial means. Finally, in 1899 Jacques Loeb succeeded in finding a method of *artificial parthenogenesis*, as the experimental activation of an egg that normally unites with a spermatozoön is called. A few years later Loeb was able to rear to maturity frogs that had developed from artificially activated eggs; these frogs had a mother but no father. It is now known that a variety of methods will initiate development in eggs that normally develop only after fertilization. George Lefevre, Sr., in 1907 used dilute organic acids (Fig. 78); others have used heat, shaking, pricking of the surface of frogs' eggs, and various chemical agents. Most of the studies on artificial parthenogenesis have been on the eggs of invertebrates, but in recent years attempts

have been made, with some success, to activate mammalian eggs artificially. It has been stated that parthenogenesis occurs normally in some insects, notably bees and aphids, and among the rotifers. Parthenogenesis, whether normal or artificial, can be induced only when the egg cell is in a certain stage, which may be called a fertilizable condition, and corresponds only to the activation aspect of fertilization. There is only one parent, and amphimixis cannot occur.

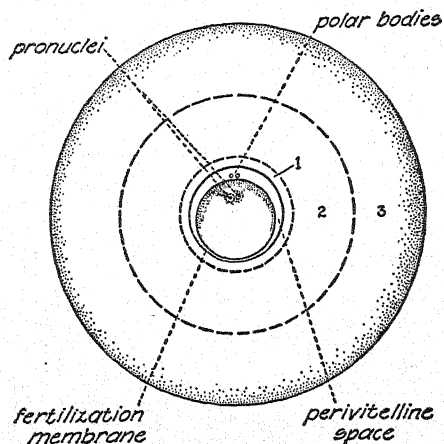


FIG. 79. The frog's egg after laying and activation, but before amphimixis has occurred. 1, 2, and 3 are the jelly envelopes.

(After O. Schultze, from H. E. Ziegler, "Lehrbuch der vergleichenden Entwicklungsgeschichte," 1902.)

Fertilization depends not only on the fertilizable condition of the egg but also on the ability of the spermatozoa to come in contact with the egg. The flagellate spermatozoön of vertebrates swims by lashing its tail; fertilization can occur only in liquids. The lower vertebrates, such as the frogs, typically copulate as the eggs are passed from the body of the female, so that the spermatozoa are shed over the egg mass in the water. Fertilization takes place in the water, outside the body. In vertebrates that live on the land, fertilization is internal. Copulation occurs, and spermatozoa are introduced into the reproductive tract of the female, where they can swim in the seminal fluid and in the liquid filling the female ducts. The spermatozoa pass into the Fallopian tubes and meet the eggs as they are ovulated. In most reptiles and birds, additional food material in the form of albumen is secreted about the fertilized egg, or zygote, as it passes down the oviduct. A shell, which prevents drying and serves as a protection for the developing individual, is added before the egg is laid or passed out of the

female's body to develop (Figs. 72 and 73). The mammalian zygote is retained in the uterine portion of the oviducts during the developmental period.

Usually only one spermatozoön penetrates an egg cell, but in some vertebrates, such as the birds, *polyspermy* is a normal occurrence; that is, several spermatozoa enter each egg. However, the nucleus of only one of these spermatozoa fuses with the egg nucleus in amphimixis.

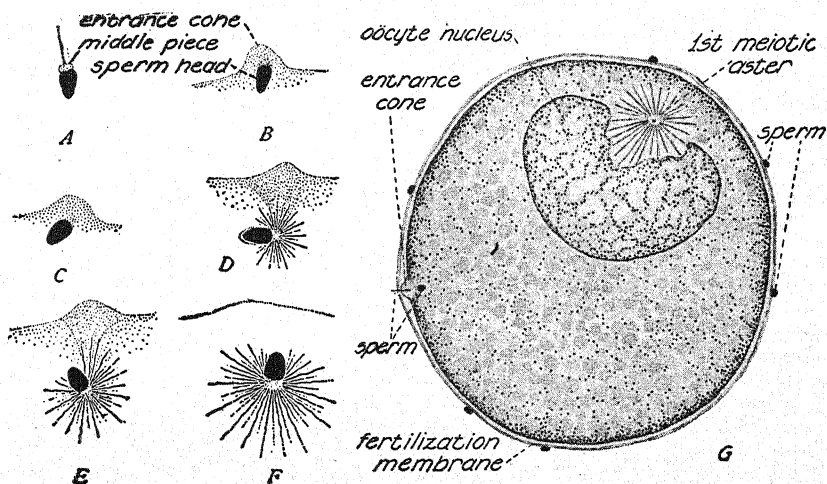


FIG. 80. Entrance of spermatozoa. A-F, entrance of sperm and rotation of the head and middle-piece in the egg of *Toxopneustes*, a sea-urchin; the fertilization membrane is not shown. G, entrance of sperm and formation of first meiotic spindle in the egg of *Thalassema* (cf. Fig. 78). A-F, $\times 1480$; G, $\times 710$.

(A-F from E. B. Wilson, "The cell in development and heredity," copyright, 1897, by The Macmillan Co., reprinted by permission.)

In 1875 Fol observed that, as soon as one spermatozoön had reached the egg, a membrane, known as the *fertilization membrane*, was usually lifted from the surface of the egg, leaving a *perivitelline space* around the egg (cf. Fig. 66, p. 119, and Figs. 76 and 79). The fertilization membrane was believed by many students to be a device to prevent polyspermy but is now recognized as a by-product of activation. Such a membrane is formed when eggs are artificially stimulated to develop (Fig. 78). The spermatozoön swims actively until it comes in contact with the surface of the egg; the egg then engulfs the spermatozoön after first sending out a minute projection, the *entrance cone*, in which it becomes embedded (Fig. 80). The process of engulfing the spermatozoön requires only a few seconds in many animals, although it may take as long as an hour. Most often the tail of the spermatozoön is not

taken into the egg; only the head containing the male pronucleus and the middle piece containing the centriole, which gives rise to the centrioles of the spindle of the zygote, are involved in fertilization (*cf.* Fig. 66, p. 119, and Figs. 76 and 80). The tail of the spermatozoön undergoes degeneration as development begins when the tail enters the egg; this happens in the bat, the frog, and some other animals.

Development

Reproduction in the vertebrates is complete when maturation, activation, and amphimixis have taken place, when the differentiated egg and sperm cells have united. The zygote is potentially a new individual; it has the capacity to develop into a being in all essential respects like its parents. The process of development, which always follows reproduction by syngamy in the multicellular animals, consists essentially of cell division, cell localization, and cell differentiation. Growth occurs in all developing individuals and is responsible for the increase in the amount of protoplasm that is correlated with the increase in cell numbers by continued cell division. Development is a continuous process in which a definite series of events occurs in a definite sequence under very limited environmental conditions. Food and oxygen are furnished, excretions are removed, excessive loss of water is prevented, and a rather limited temperature range is maintained. The methods of caring for the metabolic requirements of a developing individual will be discussed later (p. 150), but it may be noted here that undue evaporation is prevented during the development of terrestrial vertebrates by egg-membranes and shells or by the retention of the embryo in a uterus. The range of temperature is determined roughly in fishes, amphibians, and reptiles by the season at which the eggs are laid, and unseasonal temperatures kill such developing eggs. Birds, of course, incubate their developing eggs; in mammals the mother's body regulates the temperature of the embryos in the uterus. In our discussion of development we shall assume that all environmental conditions are normal. The development of a single cell into a complex, highly differentiated animal is one of nature's marvelous pageants, a series of events that occurs in such an orderly fashion as to fill the observer with awe.

The pattern of early development is correlated very closely with the amount of nutritive material stored in the oöcyte during its growth period in the ovary. In the Chordata there is a wide range in the quantity and position of the yolk in eggs. The amphioxus, for example, has an *isolecithal egg*, so called because the relatively

small amount of reserve nutrients is distributed almost uniformly throughout the cytosome. Among the vertebrates the frog has a *telolecithal egg* in which a considerable quantity of yolk is stored more abundantly in one half, the so-called *vegetal hemisphere*, than in the other half, or *animal hemisphere*, in which the nucleus is always found (Fig. 72). A more pronounced polarization of nucleus and yolk is to be seen in the telolecithal eggs of fishes, reptiles, and birds (Fig. 73). In such eggs the nucleus is located near the animal pole surrounded by a relatively small amount of cytoplasm forming the *blastodisk*, and the large cytosome is packed with yolk enclosed by a very thin layer of cytoplasm, which lies at the surface of the egg. The egg-laying mammals produce telolecithal eggs like those of reptiles; the placental mammals have isolecithal eggs in which varying amounts of reserve nutrients are stored but never in large quantity. The mouse's egg, for instance, has only chondriosomes as storage material; in bats and swine, fat and yolk compounds are stored (Fig. 77).

As the sequence of events during the development of chordates is described, comparisons will be made between certain representative forms in such a way as to call attention to the fundamental similarity of development in all, as well as to indicate special differences. Development is a continuous process, although it can be divided into stages for purposes of discussion. In the account which follows, the early stages that are characterized only by cell division are described under that heading. The stages during which the conspicuous mass movements of cells that separate the so-called germ layers and establish the body-plan, as well as the primordia of all the organ-systems, are occurring are described under the heading of cell localization. The final stages in which cytosomal differences appear in cells, with the production of tissues, are summarized under the heading of cell differentiation.

Cell Division: Cleavage. Cleavage follows activation and consists of a series of cell divisions. Cell division, of course, occurs during other periods, but during cleavage it is the only visible indication of development. What we see externally is the constriction of the cytosome during the telophase of mitosis; the orderly separation of half-chromosomes occurs before this. During the early divisions all the cells divide at so nearly the same rate that it appears as if the zygote were being cut with a knife into smaller and smaller parts. If the zygote is visualized as a globe with the north pole of the earth representing the animal pole of the zygote and the south pole representing the vegetal pole, it may be easier to understand how the zygote is divided during cleavage.

In the amphioxus (*Branchiostoma lanceolatum*) cleavage is *total*; that is, the entire zygote is divided into two cells of the same size, and division continues to produce cells that differ but little in size (Figs. 76, 77, and 81 B and C). The cleavage pattern is like that of the frog, in which cleavage is also total but in which inequality in the sizes of cells is soon apparent. In the frog the plane of the first

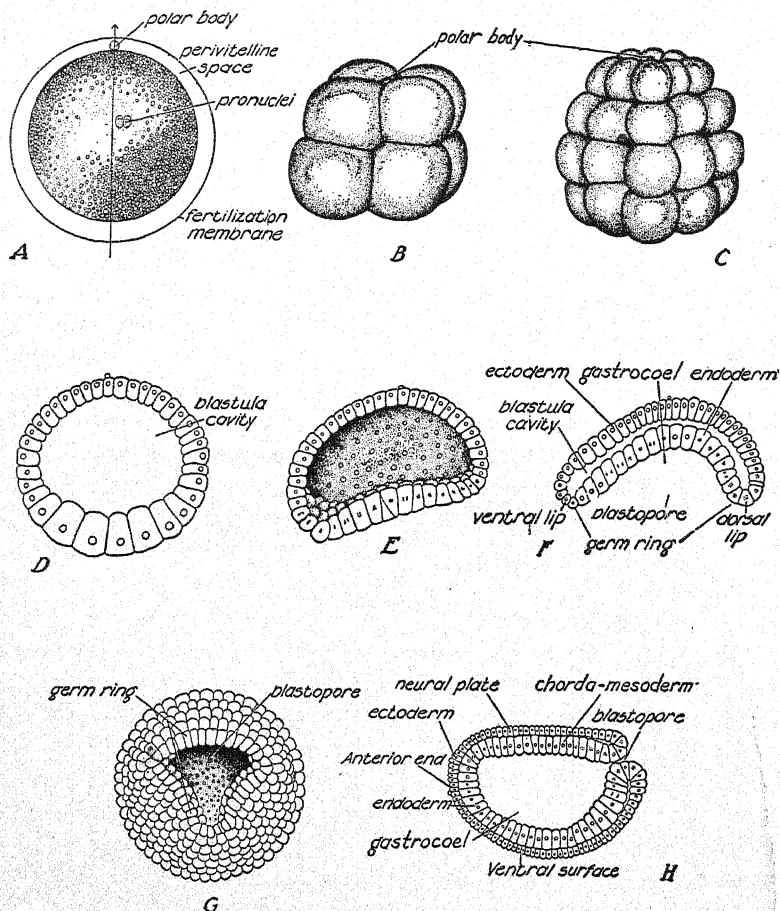


FIG. 81. Early development in the amphioxus. A, one-cell stage, in section; the arrow indicates the egg-axis. B, eight-cell stage, from the surface. C, thirty-two-cell stage, from the surface. D, early blastula, in section. E, late blastula, as if cut in half. F, early gastrula, in section. G, gastrula, from the surface. H, late gastrula in section, oriented to show dorso-ventral and antero-posterior axes.

(A, B, and G, from E. G. Conklin, 1933, Jour. Experimental Zoölogy, vol. 64; C-F and H from E. G. Conklin, 1932, Jour. Morphology, vol. 54.)

cleavage furrow, as the cytosomal constriction is called, passes from the animal to the vegetal pole. Usually one of the resulting cells is destined to give rise to the right side of the individual, the other to the left side. This fact has been established because of certain changes that occur in the frog's egg after the entrance of the sperm. The sperm enters at some point in the animal hemisphere, and as the second meiotic division occurs, streaming movements in the cytoplasm result in a distribution of material with reference to the plane of entrance of the sperm and the path it follows as it is carried toward the egg nucleus (Fig. 82 A and B). These streaming movements of the cytoplasm, in addition to producing invisible localization of cytoplasmic regions, give rise to the *gray crescent*, an area from which some of the pigment is carried away, which lies approximately opposite the entrance point of the sperm. With this visibly different region as a landmark, observations can be made concerning the fate of certain regions of the zygote during development. Thus it has been determined that the future median longitudinal plane of the embryo coincides with a plane passing through the egg-axis and bisecting the gray crescent (Fig. 82 B). Since the first cleavage plane usually bisects the gray crescent, it follows that bilateral symmetry becomes apparent at this time.

The second cleavage furrow likewise appears first at the animal pole and passes to the vegetal pole at right angles to the first, so that a four-cell stage results. These cells are of equal size, but cleavage now becomes unequal in the frog. The third cleavage furrow cuts each of the four cells in a plane parallel to the equator but nearer the animal than the vegetal pole. Of the resulting eight cells, the four in the animal hemisphere are smaller. Two fourth cleavage furrows appear simultaneously in the smaller cells and pass through the larger cells to form a sixteen-cell stage. After this, two fifth cleavage furrows, one on each side of the third cleavage furrow, produce thirty-two cells. Indications of an irregularity of division rate can often be seen during the fourth and fifth cleavages, since the furrows pass more rapidly through the cells containing less yolk. This difference in rate of division is an important factor in later development.

Formation of the Blastula. As the egg divides during cleavage, the cells tend to become spherical. Since the amount of yolk stored in the female germ cell is being utilized as the source of energy for cleavage, a small cavity appears internally as early as the eight-cell stage in the frog. This cavity is quite conspicuous after the fifth cleavage and is known as the *cleavage cavity*, *blastula cavity*, or *blastocœl*. The developing individual is now called a *blastula*, and this period

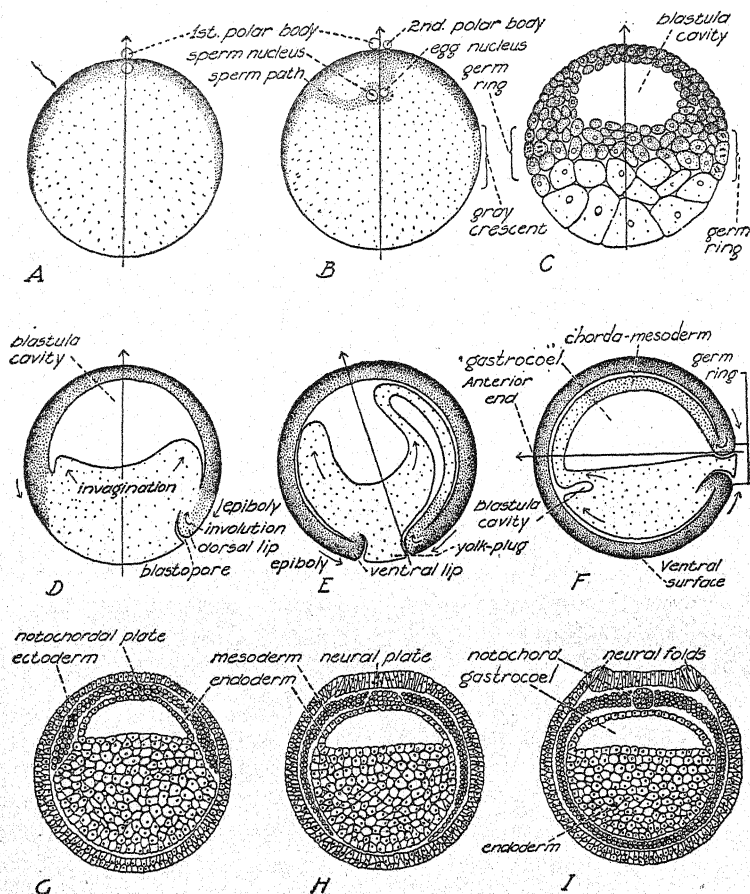


FIG. 82. Early development in the frog. *A*, egg before activation, in section. *B*, one-cell stage before amphimixis, in section (*cf.* Fig. 79). The first cleavage furrow would pass in the plane of the paper, through the egg-axis, and bisect the gray crescent. *C*, late blastula, in section. *D*, early gastrula, in section. *E*, gastrula in section. *F*, late gastrula, in longitudinal section, oriented to show dorso-ventral and antero-posterior axes. *G*, *H*, and *I*, embryos during the formation of the notochord, the dorsal mesoderm, and the neural plate, in cross-section. All figures diagrammatic; the arrow indicates the egg-axis.

(*E* and *F*, redrawn with modifications from R. S. McEwen, "Vertebrate embryology," copyright, 1931, by Henry Holt and Co., printed by permission.)

in development is referred to frequently as the *blastula* stage. The blastula arises as a result of cell division only; no cell movements have occurred. If the egg is isolecithal and cleavage is total and approximately equal, the blastula cavity is located centrally and sur-

rounded by cells of similar size, as in the amphioxus (Fig. 81 D). In the amphibians, where the egg is telolecithal and cleavage is total but unequal, the blastula cavity is in the animal hemisphere and has a roof of small cells and a floor of large cells (Fig. 83 A). Further, in the fishes, reptiles, and birds in which the egg is telolecithal and cleavage occurs only in the blastodisk, or small amount of cyto-

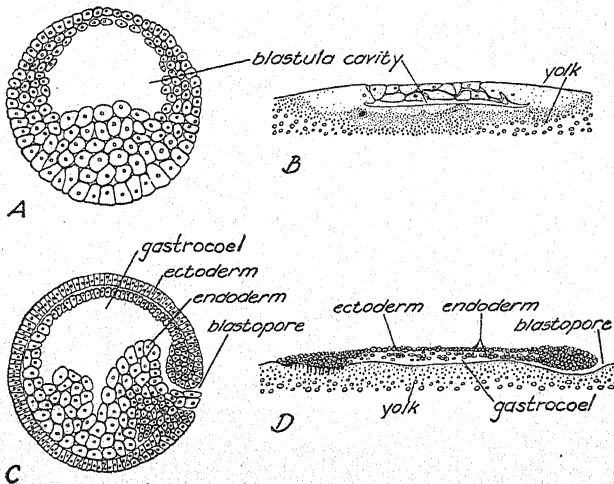


FIG. 83. Blastulae and gastrulae of amphibians and birds. A, blastula of *Triton*, a salamander. B, blastula of the domestic fowl. C, gastrula of *Triton*. D, gastrula of the pigeon (cf. Fig. 62, p. 114, and Fig. 283, p. 394).

(A and C, redrawn from O. Hertwig, "Lehrbuch der Entwicklungsgeschichte des Menschen und der Wirbelthiere," 1890; B, redrawn from J. T. Patterson, 1910, Jour. Morphology, vol. 21; D, redrawn with modifications from J. T. Patterson, 1909, Jour. Morphology, vol. 20.)

plasm surrounding the nucleus at the animal pole, the blastula cavity lies between the disk of cells and the underlying, undivided yolk-mass (cf. Figs. 73 B and C and 83 B). The blastula cavity in forms like the amphibians and birds is filled with a solution of food material that diffuses into it from the yolk-laden cells or yolk-mass that forms its floor.

Cell division continues during the blastula stage. In the frog the cells divide parallel to the surface of the blastula so that the blastula cavity becomes roofed by several layers of cells. Also, the difference in rate of division becomes increasingly obvious until the cells in the equatorial region are dividing more rapidly than the cells in other regions. This equatorial belt of cells, which is not visibly different from other parts of the animal hemisphere, is known as the *germ ring*

and plays a very important rôle in later development (Fig. 82 C). The cells formed by the rapid division in this region spread toward the vegetal pole. Since these cells are pigmented, the direction and extent of their movements can be noted; the original location of the gray crescent can still be observed. The establishment of the germ ring and the beginning of its shift in position mark the end of that part of development in which cell division is the characteristic event. Cell division, however, continues, and the number of cells increases greatly during the next period of development.

Cell Localization. The spread of cells formed at the original equatorial region of the zygote toward the vegetal pole is the beginning of a phase of development characterized by mass movements of cells which lead to the establishment of the so-called body-plan of the chordate. During this period of cell localization masses of cells are brought into new relations with one another. The embryo is presently found to consist of three distinguishable layers of cells which have long been called the *germ layers*, namely, *ectoderm*, *endoderm*, and *mesoderm*. The first part of cell localization is frequently referred to as gastrulation.

Gastrulation in the amphioxus is a much simpler process than in the amphibia, where the yolk-laden cells are a complicating factor in the movements that occur. In the amphioxus the late blastula becomes somewhat flattened at the vegetal end, the cells of which begin to enter the blastula cavity (Fig. 81 E-H). This is known as the process of *invagination* and is influenced by the higher rate of cell division at the margin of the original flattened area of the blastula; this margin is the germ ring. The rapid increase in number of cells in the germ ring crowds the plate of vegetal cells until a shift in position takes place. The germ ring is also known as the *lips* of the *blastopore*, which is the open end of the early *gastrula*, as the developing individual is now called. The movements of the cells continue until the blastula cavity is obliterated completely and there is a new internal cavity, the *gastrula cavity*, *gastrocoel*, or *archenteron*, which opens externally by way of the blastopore. As a result of the shifting of cells the individual now consists of two layers of cells, an outer layer of *ectoderm* and an inner layer containing the primordia of the other two germ layers, which will be sorted out by subsequent movements. The outer and inner layers are continuous with one another in the region of the germ ring, that is, at the lips of the blastopore. Continued cell divisions in the germ ring add cells to both these layers, and the gastrula becomes elongated as the germ ring decreases in circumference. This decrease in size of the germ ring is also known as the closure of the blastopore,

which becomes smaller and smaller. This stage in the development of chordates is suggestive of the so-called diploblastic, or two-layered, body-plan of coelenterates (*cf.* pp. 232 and 336).

Gastrulation in amphibia is essentially the same as in the amphioxus. Increase of cells in the germ ring tends to push the yolk-laden cells into the blastula cavity and produce invagination, but this is not the rapid and conspicuous process that it is in the amphioxus because of the heavy yolky cells (Fig. 82 D). A more noticeable result of the division of cells in the germ ring is its overgrowth of the cells of the vegetal hemisphere, so that the pigmented area increases, whereas the non-pigmented area decreases in extent. As the overgrowth occurs, the region of the gray crescent can still be identified, and at the pigmented border of this region an inturning of cells begins. In other words, the cells derived from the gray crescent come to lie inside the gastrula in the region of the dorsal lip of the blastopore and in what is to be the mid-dorsal region of the embryo. The part of the germ ring in which division is most rapid is the part from which inturning first occurs and which is known thenceforth as the dorsal lip of the blastopore, or the opening into the gastrocoel. Soon the process of inturning, or *involution*, occurs along the entire margin of the germ ring, which thus becomes the lips of the blastopore. In the amphibia the blastopore is plugged with the cells of the vegetal hemisphere which have not shifted their position (Fig. 82 E). The overgrowth of the yolk-laden cells by the germ ring is known as *epiboly* and continues, with the resulting decrease in the circumference of the germ ring and in the area of the yolk-plug, until the yolk-plug is covered and the blastopore is a minute opening. Internally, the gastrula cavity increases greatly in extent as a result of invagination and involution, whereas the blastula cavity decreases in size as the gastrula cavity expands. As gastrulation progresses, it is possible to distinguish dorsal and ventral surfaces, as well as anterior and posterior ends, because of their subsequent development. Furthermore, the expansion of the gastrula cavity in the dorsal half of the gastrula and the obliteration of the blastula cavity in the animal hemisphere result in a rotation of somewhat more than 90° in the position of the individual within its jelly envelopes. Instead of the animal hemisphere, the dorsal half now floats uppermost.

As the blastopore closes in amphibia, the shift of cells from an external to an internal position is completed. The cells which remain on the surface are the ectoderm; those which have moved in and now line the gastrocoel dorsally and laterally are the presumptive notochord and mesoderm. Farther down along the sides of the gastrocoel the in-

wardly shifted cells are the true endoderm. In the floor of the gastrula cavity these cells receive additions from the yolk-laden cells by a process of *delamination*, or rearrangement, to form a definite layer. Laterally, at the junction between the endoderm and the presumptive mesoderm, a separation occurs between the two. Division of cells in each region extends the layers. The two sheets of endoderm move

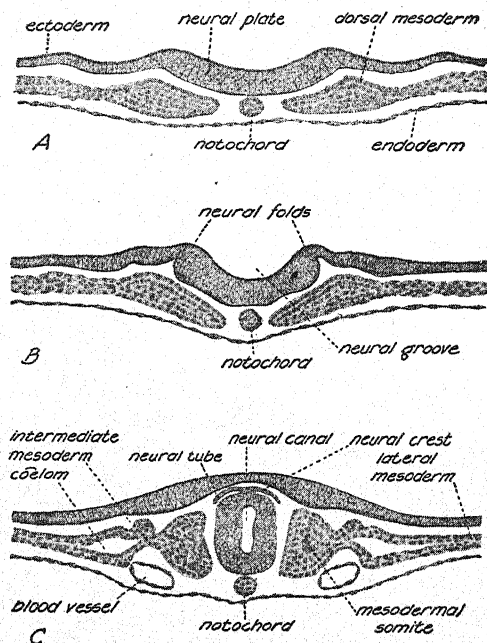


FIG. 84. The localization of the neural tube in the domestic fowl. A, B, and C, successive stages, in cross-section.

(Redrawn with modifications from M. Duval, "Atlas d'embryologie," 1889.)

dorsally until they meet one another in the mid-dorsal line to form a continuous lining for the gastrula cavity. This makes the presumptive mesoderm a middle layer, the true *mesoderm*, lying between the ectoderm and endoderm. Its free ventral margin on each side extends until the two sheets meet mid-ventrally. Dorsally, the mesoderm is continuous with a median mass of cells derived by involution from the dorsal lip of the blastopore (Fig. 82 G). This association constitutes the *chorda-mesoderm*. Presently the sheets of the mesoderm are no longer continuous with the mid-dorsal cells, which become arranged as a longitudinal cord of cells known now as the *notochord* (Fig. 82 H and I). Somewhat later the characteristic cavity of the mesoderm

appears; this is the *cœlom* (cf. Fig. 84). With the localization of the three germ layers and the formation of the archenteron and the *cœlom* as cavities surrounded, respectively, by the endoderm and the mesoderm, the fundamental triploblastic body-plan of the chordates has been established.

The establishment of the typical body-plan is only the beginning of cell localizations. Within each of the three layers movements of lesser masses of cells occur and give rise to the primordia of the organ-systems of the adult vertebrate.

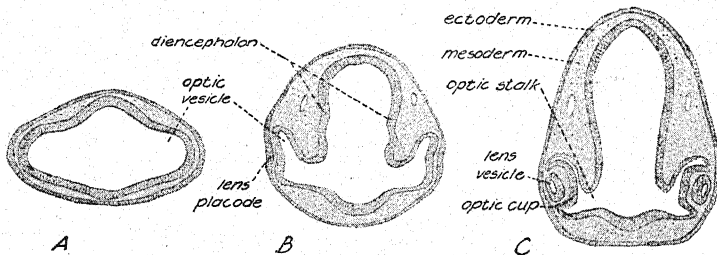


FIG. 85. The early development of the eye. A, B, and C, cross-sections through the heads of chick embryos, showing successive stages in the localization of the various parts of the eye.

At the same time that the mesoderm and notochord are being localized, the first stage in the formation of the *nervous system* occurs. The ectoderm over the chorda-mesoderm becomes thicker and is known as the *neural plate* (Fig. 82 H). Along the lateral edges of this thicker plate of ectoderm, where it is continuous with the thinner ectoderm, folds appear on the surface of the embryo. These are the *neural folds*, which move toward the dorsal midline, where they meet and fuse. This fusion unites not only the edges of the neural plate to form the *neural tube* but also the edges of the thinner *superficial ectoderm* that covers the entire surface of the frog embryo and gives rise to the epidermis of the skin (Fig. 82 I and cf. Fig. 84). During the closure of the neural folds some ectodermal cells are left between the superficial ectoderm and the neural tube; they form the *neural crest*. The neural plate is wider at its anterior end than it is toward the blastopore, and the neural tube is consequently larger at the anterior end. Thus, from a very early period, the anterior region is distinguishable as the part destined to give rise to the *brain*, and the posterior part is marked as the region which is to give rise to the *spinal cord* (Figs. 86 and 87). Within the brain region localized expansions produce first

three and then the five *brain vesicles* which are characteristic of all vertebrate embryos (cf. Fig. 89 and p. 62).

The formation of the eye occurs at the time when the brain vesicles are established in vertebrates. Near the anterior end of the brain, expansions appear to the right and left; these are the *optic vesicles*

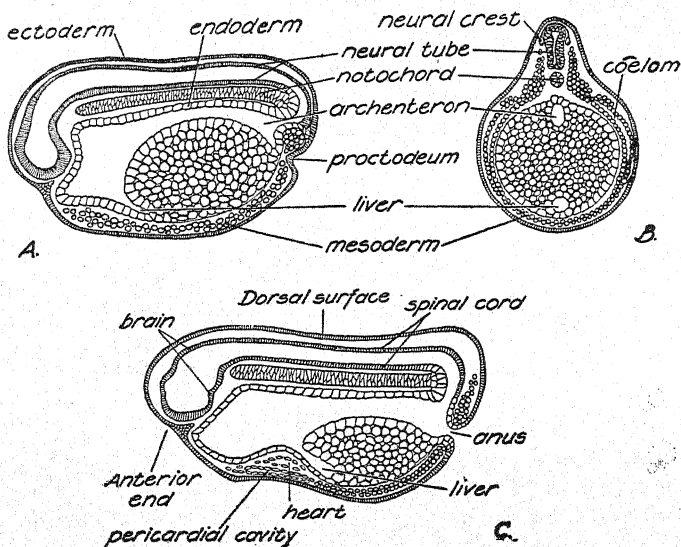


FIG. 86. Young tadpoles of the frog, to show localization of organ-system primordia. A, tadpole of about hatching age, in longitudinal section. B, later tadpole, in cross-section; and C, later tadpole, in longitudinal section (cf. Fig. 87 E and F). All sections diagrammatic.

(A, redrawn from T. H. Morgan, "The development of the frog's egg," copyright, 1912, by The Macmillan Co., printed by permission; C, redrawn from J. W. Jenkinson, "Vertebrate embryology," copyright, 1913, by the Oxford University Press, printed by permission.)

(Fig. 85). Later the outer cells of these vesicles fold in to produce the *optic cups*. At the same time the superficial ectoderm covering the optic cup thickens and folds in to form the *lens vesicle*, which is later cut off and forms the *lens* of the eye (cf. Fig. 85 B and C and Fig. 34, p. 65).

The primordium, or first indication of the *digestive system*, is distinguishable when the endoderm and archenteron are formed, although the blastopore does not persist as the posterior opening of the alimentary canal. A depression of the superficial ectoderm occurs posteriorly to form the *proctodeum* and anteriorly to form the *stomodeum* (Figs. 86 A and 87 D and E). These pits, which are lined with

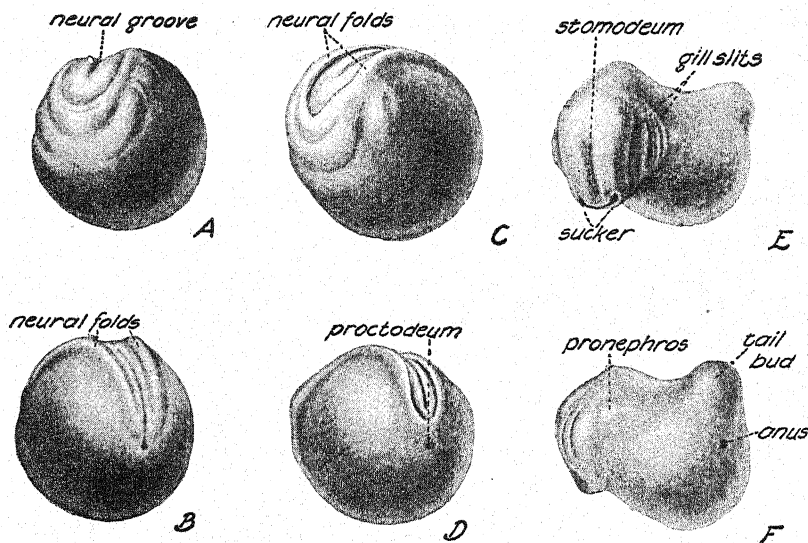


FIG. 87. Young tadpoles of the frog, showing changes in shape. A, C, and E are successive stages, viewed from the anterior end and left side. B, D, and F are comparable stages, viewed from the posterior end and left side.

(A-E, redrawn from R. Bonnet, "Lehrbuch der Entwicklungsgeschichte," 1907.)

ectoderm, become the most posterior part of the digestive tract and the mouth cavity, respectively (*cf.* p. 25). The *liver* and *pancreas* arise as outgrowths from the archenteron and are lined with endoderm. Closely associated with localizations related to the digestive system are those of the *respiratory system*. In the pharyngeal region of the alimentary canal paired pouches extend to the surface ectoderm, in which slits appear (*cf.* Figs. 87 and 88 A). These *gill slits* or *clefts* make possible a flow of water through the pharynx in adult fishes and certain amphibians, including the tadpole of the frog. *Gills*, or organs of external respiration, are developed later in this region. Such pharyngeal

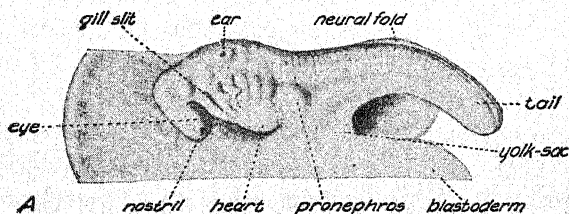


FIG. 88. Embryo of the torpedo, an elasmobranch, attached to its yolk-sac.

(Redrawn from H. E. Ziegler, "Lehrbuch der vergleichenden Entwicklungsgeschichte," 1902.)

pouches and at least vestigial gill slits are characteristic of all chordate embryos (*cf.* Fig. 89 and Fig. 496, p. 682). In terrestrial vertebrates the *lungs* and *air-tubes* are also formed by an outgrowth from the endoderm lining the pharyngeal region of the primitive gut.

The mesoderm undergoes many changes in the period after its localization. Most conspicuous is the proliferation that occurs along the

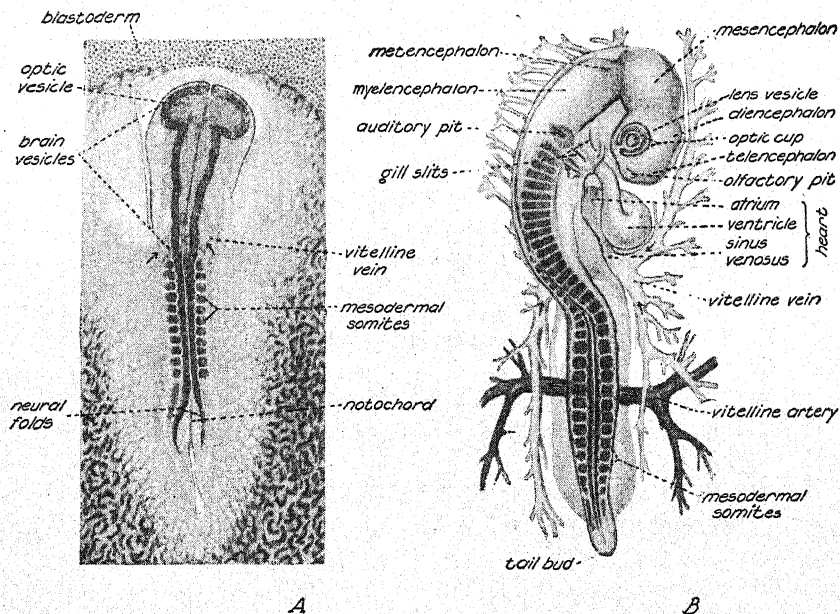


FIG. 89. Chick embryos, showing localization of organ-system primordia; dorsal view. *A*, embryo after twenty-nine hours' incubation. *B*, embryo after fifty-two hours' incubation, with its embryonic membranes removed. Internal structures are shown as if seen through the surface.

(Redrawn from M. Duval, "Atlas d'embryologie," 1889.)

sides of the neural tube, forming what is called the *dorsal mesoderm*, or *epimere*. Soon these cords of mesoderm become segmented and give rise to the *mesodermal somites* (Figs. 84 and 86). Later, after continued cell division, the cells of the somites are shifted in position. Some migrate around the notochord and neural tube and later form the vertebral column. Others make up the muscle plates, from which the *striated muscles* of the trunk arise, while still others form the *dermis* of the skin. Lateral to the dorsal mesoderm on each side there is a region called the *intermediate mesoderm*, or *mesomere*, in which the *excretory* and *reproductive systems* are differentiated (Figs. 84 C and

86 B). The remaining mesoderm is the *lateral mesoderm*, or *hypomere*, the cells of which become rearranged into an outer layer lying close to the ectoderm and an inner layer next to the endoderm (Figs. 84 B and C and 86 B). The cavity of the hypomere lying between these two layers is the *cœlom*. The heart and main vessels of the *circulatory system* are established in the mesoderm (Figs. 89 and 86 C).

In all these localizations of cells from the initial shift in position of the germ ring, the movements are correlated with an unequal increase in number of cells, conditioned by a rate of cell division that is higher in one region than in neighboring regions. Sometimes ingrowth into an available space occurs, as in gastrulation and the formation of the lens vesicle; sometimes an outgrowth results, as in the origin of the optic vesicle and the liver. If space is available, a uniform expansion of a region of rapidly dividing cells may occur, as when the brain vesicles are formed and the stomach begins to enlarge.

Localization		Differentiation
Germ Layers	Systems and Organs	Tissues
Ectoderm	Nervous system Eyes, ears, and nasal cavities Epidermis of the skin Lining of the proctodeum and stomodeum	Nervous tissue Epithelial tissue
Mesoderm	Dermis of the skin Skeletal system Wall of the digestive tract, except the lining Muscular system Circulatory system Excretory system Reproductive system Lining of the cœlom	Sustentative tissue Contractile tissue Vascular tissue Epithelial tissue
Endoderm	Lining of the digestive system, except in the region of the stomodeum and proctodeum Lining of the lungs and air-tubes	Epithelial tissue

FIG. 90. The principal localizations of cells and their differentiation during the development of the vertebrates.

Localizations occur in different regions at the same time, but in a very orderly manner. The same degree of localization will be found in any vertebrate embryo of a given species at a given age. Under normal environmental conditions developmental processes occur with the precision of a perfect machine.

Cell Differentiation. During the various movements of masses of cells in relation to their neighbors that occur as localization takes place, no essential changes in the character of the cells can be noted. However, when a group of cells has finally shifted its position, cell differentiation, or *histogenesis*, begins; that is, the cytosomal changes that give rise to the tissues of the adult occur. The differentiation or specialization of the tissue cells will not be described in detail here. By reference to Figure 90 you can correlate the localizations and differentiation of development with the anatomy and histology of the adult vertebrate.

Metabolic Requirements of Embryos

The orderly series of changes which occurs during development depends upon reactions that take place in the protoplasm, and these, in turn, upon the metabolic requirements of the protoplasm. A constant supply of food and oxygen must be available, and waste products of dissimilation must be eliminated. The temperature, which is one factor conditioning the rate of metabolism, cannot vary widely, and drying must be prevented.

In the frog embryo, which has been used to illustrate the course of development in vertebrates, these metabolic requirements are met simply. A large amount of food is stored in the egg, the egg is laid in water from which oxygen is obtained by diffusion, and the breeding season is so adjusted that temperature conditions are favorable for development (*cf.* Fig. 450, p. 615). The frog embryo within the fertilization membrane is protected from adhesions, and there are no so-called embryonic membranes. As the localization of the primordia of organ-systems occurs, a U-shaped *sucker* appears on the ventral surface of the head of the frog embryo, and a median posterior extension foreshadows the formation of a *tail* (Fig. 87). The embryo hatches by slipping out of its disintegrating jelly envelopes and becomes attached to objects in the water by means of the sucker. When the stomodeum becomes continuous with the pharynx and the tail is developed further, the individual swims and feeds, although it does not resemble an adult frog. Such a self-supporting but not fully developed individual is called a *larva*; the larva of the frog is known as a *tadpole*. During

the tadpole stages the frog feeds upon plants and carries on external respiration by means of its gills, of which there is first an external and then an internal set (*cf.* Fig. 88 and Fig. 450, p. 615). Toward the end of the tadpole period in development the animal begins a *meta-*

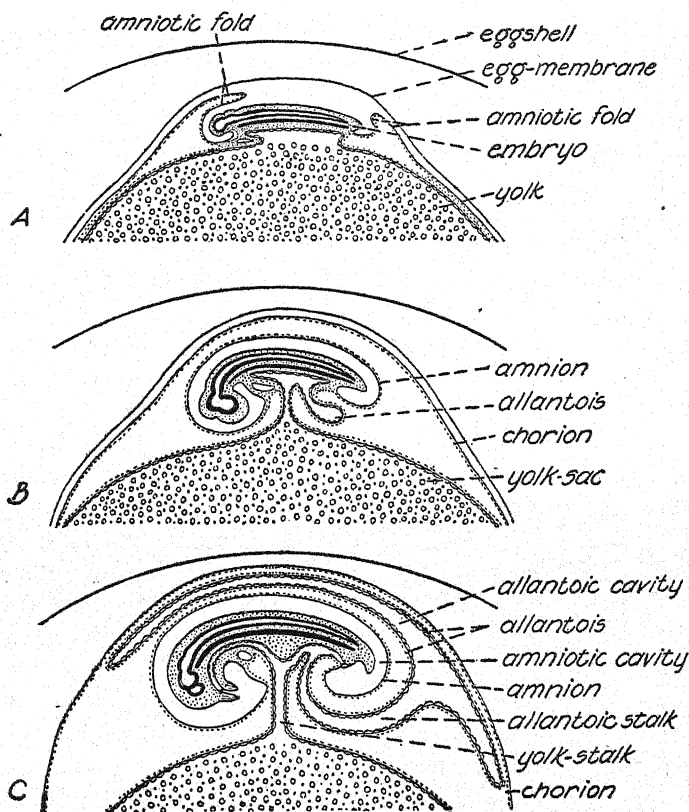


FIG. 91. The embryonic membranes of the chick. A, B, and C, diagrams of longitudinal sections of successive stages during development.

(Redrawn with modifications from T. J. Parker and W. A. Haswell, "Textbook of zoölogy," copyright, 1921, by Macmillan and Co., Ltd., printed by permission.)

morphosis, or change from larval to adult structure. Hind legs and then front legs appear and grow, the tail decreases in size until it disappears, and the mouth and jaws become like those of the frog. The lungs become functional, and the gills disappear. In correlation with the change from a plant diet to an insect one the intestine becomes much shorter during the period of metamorphosis (*cf.* p. 28). Many frogs complete their metamorphosis about 3 months after hatching, but the

bullfrog usually passes its first winter as a tadpole. Such a larval period in the life-cycle of a vertebrate is unusual, although larval stages characterize the development of many invertebrates (*cf.* pp. 360, 420, 501, and 546).

In the fishes the telolecithal eggs are laid in the water, but there is one important difference in development as compared with that of

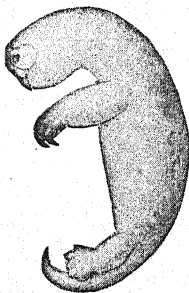


FIG. 92. An opossum embryo a few hours before its birth, showing the conspicuous development of the forelimbs which are used in reaching the abdominal brood-pouch of the mother; $\times 3$.

(Redrawn from C. H. Heuser, 1921, *American Jour. Anatomy*, vol. 28.)

the frog. Cleavage is partial, and the yolk-laden part of the zygote is not divided into cells. In correlation with this fact we find the blastoderm rapidly extending over the surface of the yolk (Fig. 88 A). The cells of the endoderm and its adjacent mesoderm form a *yolk-sac* which eventually encloses the yolk, and numerous blood vessels in this *embryonic membrane* absorb the yolk as it becomes diffusible and carry it to the developing embryo, which sometimes hatches before all its yolk is used.

The problem of meeting the metabolic requirements is much more complicated for the embryo of a terrestrial vertebrate. Certain embryonic membranes always develop in such forms. They persist only during development and serve to prevent drying, furnish food and oxygen, and eliminate excretions (Fig. 91). A yolk-sac is formed in reptiles and birds, as in the fishes, and also appears as a vestigial structure in the development of mammals (*cf.* p. 670). In addition, the *amnion* with its enclosed fluid keeps the embryo moist and provides a protective cushion, while the *chorion* forms a protective membrane next to the shell of the egg of the reptile or bird. A fourth membrane, the *allantois*, is richly supplied with blood and lies next to the chorion. The allantois is a respiratory and excretory membrane; it absorbs oxygen and eliminates carbon dioxide, both of which pass through the porous shells of reptiles' and birds' eggs.

Among the mammals the problem is again somewhat different. Some mammals lay yolky eggs as do the reptiles and birds; others store a certain amount of yolk in their eggs. The opossum, for instance, gives birth to very immature young which spend a considerable period in an abdominal brood-pouch, nourished by milk from the mammary glands (Fig. 92 and Fig. 462, p. 632). In the majority of mammals, however, practically no food is stored in the egg, and de-

velopment is completed within the uterus. This is made possible by the embryonic membranes, which are somewhat altered in function. During the early part of the period of cell localization the mammalian embryo becomes closely associated with the lining of the uterus. The amnion which is formed has a protective function comparable to that

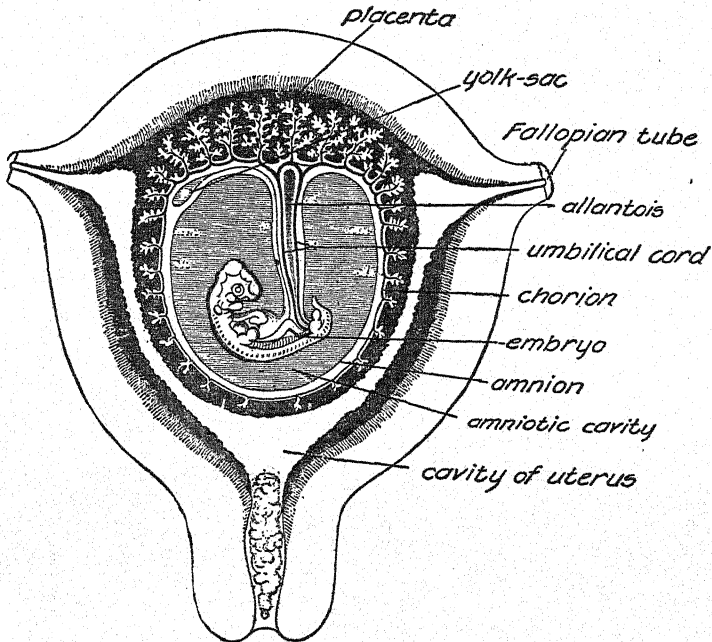


FIG. 93. The human embryo, during the eighth week of pregnancy, showing its embryonic membranes and relation to the uterus; diagrammatic.

(After A. Thomson from W. E. Kellicott, "Chordate development," copyright, 1913, by Henry Holt and Co., reprinted by permission.)

in reptiles and birds. The chorion, however, is the layer next to the tissues of the mother, and in man, for example, becomes concerned directly with nutrition, respiration, and excretion. An allantois appears during the development of the human embryo but has no function. A rich supply of blood vessels in the chorion is connected with the vessels of the embryo's body by way of vessels in the umbilical cord (Figs. 93 and 94). The chorion is covered with villi, or fingerlike processes, that extend into blood-filled spaces in the uterine wall (Fig. 95). That part of the wall of the uterus in which the young human embryo becomes embedded, together with extensions of the chorion, constitutes the *placenta*. In the placenta the blood of the embryo is everywhere

separated from the blood of the mother by the cells of the chorion, through which diffusion of nutrients, oxygen, and excretions occurs. There is no mechanism for regular exchange of blood between mother and embryo, although a certain amount of seepage probably occurs. In this connection it should be stated that the somewhat widespread ideas of prenatal impressions are entirely without foundation. The attachment between mother and embryo is such that diffusible sub-

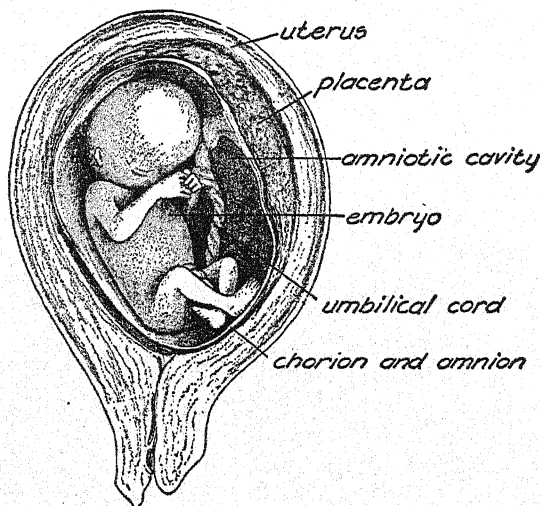


FIG. 94. The human fetus, during the fourth month of pregnancy.

(After H. Strahl from W. E. Kellicott, "Chordate development," copyright, 1913, by Henry Holt and Co., reprinted by permission.)

stances carried by the blood can pass from one to the other. There is, however, no mechanism for the transfer of emotional conditions, unless an effect on nutrition might be so produced, and no nervous connections exist whereby reactions of the mother to unpleasant sights can affect the embryo. Only metabolic conditions can be reflected by the development of the embryo. In very few instances is there any evidence of transfer of disease or poisons from the mother to the embryo in the uterus. The microorganism causing syphilis can pass the placenta and produce the disease in the fetus, as the human embryo is called after the third month. If a woman has German measles during the first three months of pregnancy, the causative agent passes the placenta and brings about severe effects in the embryo.

A striking illustration of another of the few disadvantages inherent in the intimate association of the embryo with its mother has recently

been studied. This is the origin of a very serious disease (fetal erythroblastosis) which reduces the number of red blood cells in the fetus during late pregnancy. It has been found that human red cells may have an antigen called the Rh substance in addition to A and B (*cf.* p. 100). Whether or not these antigens are present depends upon the heredity of the individual (*cf.* p. 192). Individuals who lack the Rh antigen do not normally contain an antibody for it; only 13 per cent of

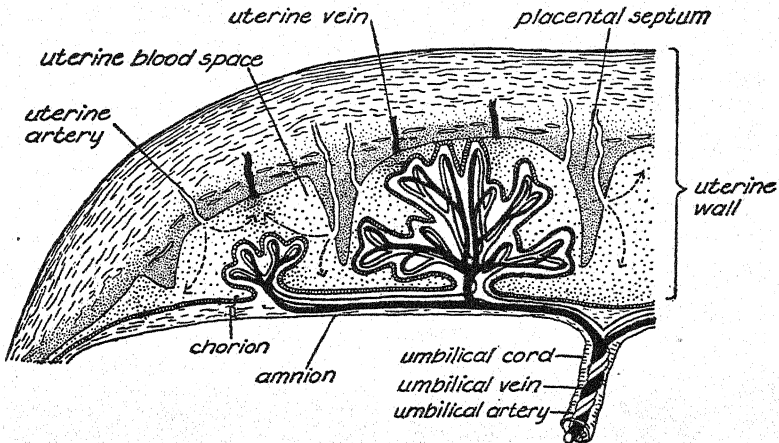


FIG. 95. A portion of the human placenta, in section, showing the relationship between the capillaries of the embryo and the blood spaces of the mother; diagrammatic.

(Redrawn from L. B. Arey, "Developmental anatomy," copyright, 1930, by W. B. Saunders Co., printed by permission.)

the general population lack the Rh antigen. If a man has the Rh substance and his wife lacks it, at least half and perhaps all of their children will produce red cells containing the Rh substance. It appears certain that enough Rh-containing red blood cells or fragments of them pass from the blood vessels of the fetus to the blood of the mother in the placenta to stimulate the production of Rh antibodies by the mother. She immunizes herself against this foreign protein, the Rh substance. These antibodies, when they have become abundant enough, begin to diffuse back through the placenta into the blood of the fetus. There they result in the destruction of the fetal red blood cells and consequently in excessive drain on the regions forming red cells, usually with fatal results. The anti-Rh substances persist in the blood of such a woman and, if her husband is homozygous (*cf.* p. 179) for Rh, make it impossible for her to bear a living child. Ery-

throblastosis results in death to the fetus or newborn infant in slightly more than 2 per cent of the pregnancies in the white population of this country.

The embryonic membranes are not permanent structures. When the reptile or bird hatches, the embryonic membranes are left in the shell. After the birth of a mammal its embryonic membranes are expelled from the uterus. The development of such structures by reptiles, birds, and mammals has made them independent of the water during development. Amphibians which are terrestrial as adults must undergo their development in the water since they have no amnion and chorion. Embryonic membranes and their modifications must have been extremely important in the evolution of the vertebrates, especially in the origin of the mammals.

Experimental Modification of Development

That the orderly processes which occur during development are conditioned by a number of closely interrelated factors can be ex-

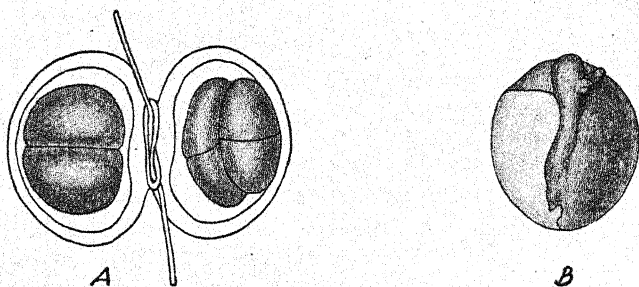


FIG. 96. Development of the frog after separation of cells and injury at the two-cell stage. A, cleavage in each part after separation of the first two cells within the jelly envelopes by constriction with a hair; each separated part gives rise to a complete embryo. B, a half embryo at the neural-fold stage, following injury to one of the first two cells by means of a hot needle.

(A, after H. Spemann, 1914, *Verhandlung deutschen zoologischen Gesellschaft*, vol. 24; B, redrawn from W. Roux, 1888, *Archiv für pathologische Anatomie*, vol. 114.)

perimentally demonstrated. The genes, or hereditary units, that a zygote carries affect its development, and certain combinations of genes have been demonstrated repeatedly to bring about death in experimental animals (*cf.* p. 198). The cytoplasm of the zygote is shifted in an orderly way by streaming movements after fertilization so that certain parts are located in particular cells during cleavage and carried into typical positions by later movements. If the zygote is subjected

to strong centrifugal force so that the cytoplasm is thrown out of its usual position, the course of development is not normal. This localization of cytoplasmic areas occurs more slowly in some animals than in others. If the first two cells of the frog embryo are separated, each gives rise to a whole embryo; but if one of the cells is injured, the other forms half an embryo (Fig. 96). In some other animals, each of the first two cells will form only half an embryo if separated.

As development progresses, certain cell masses are localized and differentiate into specific organs. That this differentiation is deter-

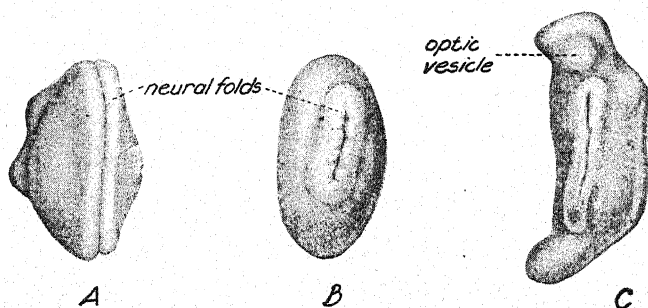


FIG. 97. Development of an embryo of *Triton*, a salamander, in which the dorsal lip of another gastrula has been transplanted ventrally. *A*, the neural-fold stage, showing the normal folds in the usual position and the folds arising over the transplanted dorsal lip at the left side; dorsal view. *B*, the same embryo viewed from the left side, so that the secondary neural folds, formed over the transplanted organizer, are more clearly seen. *C*, a later embryo, showing the secondary neural folds fused; viewed from the left side.

(Redrawn from H. Spemann and H. Mangold, 1924, *Archiv für mikroskopische Anatomie*, vol. 100.)

mined in part by the relationship of the cell mass to its neighboring cells can be demonstrated by changing the typical relationships of the cells. The ectoderm on the ventral and lateral surfaces of the frog embryo normally develops into epidermis, while ectoderm of the mid-dorsal region gives rise to the neural plate. When the dorsal lip of the blastopore is transplanted beneath the ectoderm on the ventral or lateral regions of a frog at the gastrula stage, the ectoderm covering such a transplanted dorsal lip gives rise to a neural plate, not to epidermis (Fig. 97); that is, the formation of a neural plate in the mid-dorsal region is dependent upon the localization of ectoderm cells in a certain relation to those cells of the dorsal lip that are carried internally during gastrulation. A group of cells such as those of the dorsal lip of the blastopore is known as an *organizer*, since it appears

to act as a stimulus necessary for the development of another part of the embryo. After localization is completely established in a region, differentiation is apparently independent of the influence of neighboring masses. The optic cup, for example, can be completely removed from an embryo and transferred to a test-tube containing a nutrient solution which is changed at intervals. Under such conditions differentiation of the retina will take place, although the shape of the eyeball will not be normal, since the shape of an organ depends upon the mutual pressure of adjacent cell masses. Similar indications of in-

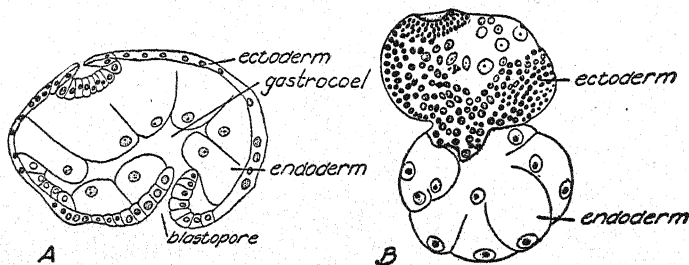


FIG. 98. Abnormal cell localization in *Crepidula*, a mollusk, as a result of an alteration in temperature. *A*, normal gastrula, in section. *B*, abnormal gastrula, in which invagination has not occurred, although ectoderm and endoderm can be distinguished.

(*A*, redrawn from E. G. Conklin, 1897, *Jour. Morphology*, vol. 13; *B*, from E. G. Conklin, "Heredity and environment," copyright, 1916, by Princeton University Press, reprinted by permission.)

dependent differentiation can be obtained by grafting parts of one embryo onto other embryos in such a way as to provide the metabolic necessities.

In addition to the relations between nucleus and cytoplasm and between masses of cells within the embryo, the conditions of the environment affect the course of development. Development normally occurs at a certain pace; anything that alters that rate produces an atypical embryo. This fact has been demonstrated in various ways. If the temperature is altered, the rate of development will be changed. When this is done at a time when some conspicuous mass movement of cells is occurring, as during the early stages of cell localization, later development may be atypical in a number of ways (Fig. 98). If the rate of metabolism is altered by decreasing the amount of food or oxygen, similar results are obtained. One such atypical effect is the production of two embryos by one zygote. Frequently such embryos are joined, but some are entirely separate; these are identical twins, which are not produced by separation of cells during early cleavage

but by some arrest of development at a later stage, probably during early cell localization. Another method of altering the metabolic rate is by the introduction of poisonous or unusual constituents into the environment. When certain salts are added to water in which fish embryos are developing, atypical localization of the optic vesicles gives rise to one median eye (Fig. 99).

It becomes obvious from these and numerous other experiments that development proceeds normally when a closely interlocking set

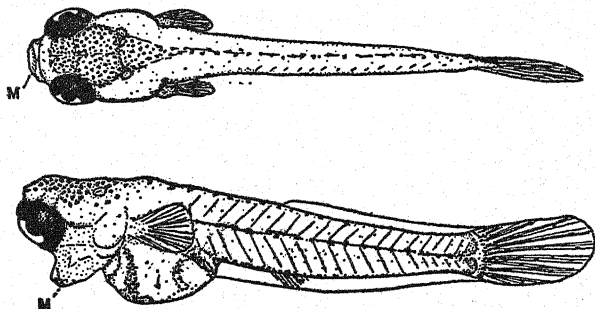


FIG. 99. Abnormal localization of the eye in *Fundulus*, a fish, conditioned by an excess of magnesium in the sea water in which development occurred. *Above*, normal embryo, from dorsal view, showing the pair of eyes posterior to the mouth (*M*). *Below*, abnormal embryo, from side view, showing the single, median eye anterior to the mouth (*M*).

(From C. R. Stockard, 1909, *Jour. Experimental Zoölogy*, vol. 6.)

of circumstances is normal. If any condition in this group is abnormal, the orderly sequence of developmental processes will be disturbed. Relations between nucleus and cytoplasm, cell mass and cell mass, embryo and external environment can be varied but slightly if a normal individual is to develop. In the developing animal, as in the adult, the protoplasm of the cells carries on its metabolism if certain conditions are normal. This protoplasm is also irritable and reacts not only to changes in neighboring cells but also to environmental changes external to the embryo. The embryo is a living individual, potentially self-sufficient at every stage in development, yet dependent, as is the adult, upon external conditions for survival. Many problems of development remain to be solved, and many new methods of research have been devised in the attack upon the unknown in this field of zoölogy. It is a fascinating and a rich field for further study.

CHAPTER 6

HEREDITY AND VARIATION

What any individual is, what it can become, and what its descendants can be like is determined by its hereditary constitution, its genetic make-up. It is often said that like reproduces like, and this statement is true in a general sense. Frogs give rise to frogs, not to toads; and dogs reproduce dogs. However, the pups of a litter are not identical with their parents nor with one another. A new individual resembles its parents, yet differs from them. The phenomena of heredity and variation go hand in hand. *Heredity* may be defined as the tendency of individuals to resemble their ancestors and relatives; *variation* is the tendency of organisms which are related by descent to differ in specific ways. New individuals arise during the process of reproduction and develop through an orderly series of changes until they reach maturity. It is obvious that whatever it is that passes from one generation to the next must determine not only the typical sequence of developmental processes but also the characteristics of the adult organism. In other words, the germ cells must carry the mechanism responsible for heredity and variation. The individual ordinarily develops under environmental conditions that are practically uniform for successive generations but cannot be ignored in seeking the complete answer to questions concerning heredity and variation. *Genetics*, a great subdivision of zoölogical science which has developed conspicuously since 1900, has for its province the subject matter relating to the facts and theories of heredity and variation.

Heredity and variation can be studied by four different methods, all of which have yielded information concerning basic problems. It is possible to observe and analyze resemblances and variations from one generation to another in large groups of individuals as they are found under natural conditions. This is the *statistical method*, or the method of *biometry*. Contrasted with such mass analysis is the observation of inheritance and variation in animals bred under experimental conditions for generation after generation. This method of *experimental breeding* under controlled conditions that give the

best environment for the organisms makes it possible to know in detail the character of heredity and variation in any particular individual, as well as to compare specifically individuals of successive generations. In order to interpret fully the result of experimental breeding it becomes necessary to study, by the method of *cytology*, the germ cells from which new individuals arise. The greatest progress in the theory of genetics has come from correlation of the results obtained from experimental breeding and such study of germ cells. A fourth way of approaching the problem of the mechanism of heredity and variation is the method of *experimental embryology*, in which individuals of known ancestry are subjected to conditions that are not usual for their development. Comparison of results obtained from these several methods of approach has yielded considerable information concerning many facts of heredity and variation and has led to the formulation of theories of the mechanism involved. Clarification and extension of our knowledge of genetics may be expected to continue in view of the great amount of interest in research in this field.

The Method of Biometry

Galton's Work. Investigators who use the biometrical method collect a great amount of observational data upon organisms under natural conditions, analyze these data by statistical methods, and formulate generalizations concerning heredity and variation that will be true for the whole group but for no particular individual. Sir Francis Galton (1822-1911) did the first serious biometrical work when he studied the relation between the height of parents and the height of offspring in over a thousand human families. From these data he proposed the laws of Ancestral Inheritance and Filial Regression (1897). According to the *Law of Ancestral Inheritance*, the parents of any individual contribute one-half of his inheritance, and the grandparents contribute one-fourth, the great-grandparents one-eighth, the great-great-grandparents one-sixteenth, and so on. The individual is, therefore, like his parents but differs from them because of the influence of more remote ancestors. The *Law of Filial Regression* is an expression of the fact that, in any large group in which considerable variation occurs, the offspring tend to be like the average and not like the extremes of the parent generation. In other words, the offspring of average parents are average; those of parents below the average are below the average; and those of parents above the average are above the average; but the offspring of parents that are either below or above the average are nearer the average than the

parents are (Fig. 100). The original study of Galton on human height has been supplemented by investigations of inheritance of eye-color, mental ability, length of life, and other characteristics by Karl Pearson, Raymond Pearl, and other biometricians.

Pure Lines and Selection. Galton's observations were made on groups that were not subjected to experimental control. His Law of

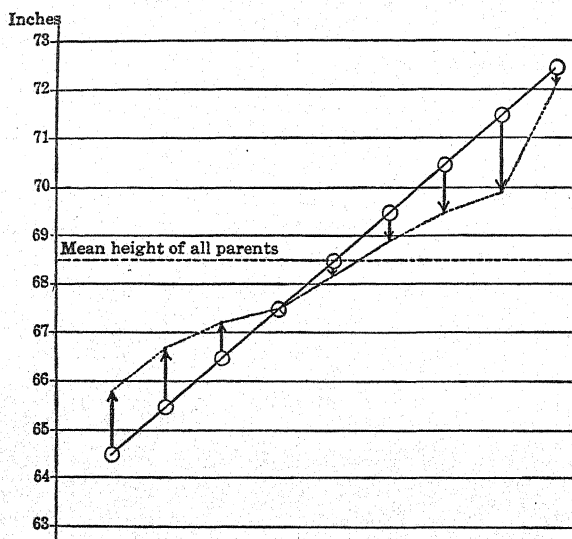


FIG. 100. Diagram illustrating Galton's Law of Filial Regression. The circles represent the height classes to which the parents belong; the arrow points indicate the average height of their respective offspring. The children of parents that are either below or above the average are nearer the average than the parents are.

(From H. E. Walter, "Genetics," copyright, 1922, by The Macmillan Co., reprinted by permission.)

Filial Regression furnished the stimulus for the experimental work of Wilhelm Johannsen, a Danish botanist (1857-1927). Johannsen conceived the idea that, if offspring of parents who were above or below the average were also above or below the average, respectively, it might be possible to shift the average by continued selection of parents from the unusual groups. Working with beans in which self-fertilization occurs, he chose the heaviest seeds from which to raise a new generation. The seeds selected weighed 80 centigrams each, and from them Johannsen obtained plants that produced seeds varying in weight from an average of 35 centigrams on some plants to an

average of 60 centigrams on others. He next tried similar experiments with the seeds from single plants. The selection of the smallest seed or the largest seed for planting had no effect on the size range of the seeds produced. It was not possible to grow larger and larger beans by planting the largest seeds time after time. Since cross-fertilization did not occur, the fundamental hereditary constitution was not altered throughout the experiment. Beans descended by self-fertilization from

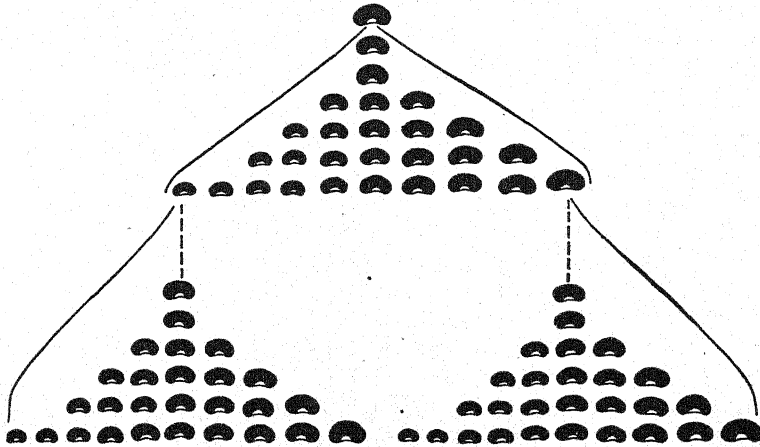


FIG. 101. Diagram illustrating the fact that selection of variations which are conditioned by environmental factors alone does not shift the average. *Above*, the size variations of seeds from a single bean plant; *below*, the size variations in progeny from the largest and smallest of these seeds.

(From E. Baur, "Die wissenschaftlichen Grundlagen der Pflanzenzucht," 1921.)

any single plant constitute what is known as a *pure line*. Within pure lines Johannsen found that, although environmental factors of temperature, moisture, or soil might affect the size range, the average weight could not be shifted by selecting either the lightest or the heaviest beans for planting (Fig. 101 and cf. Fig. 521, p. 716).

Johannsen was also able to demonstrate that in large groups of bean plants many pure lines are represented (Fig. 102). Such large groups of individuals are known as *populations*. Just as each pure line varies around its average, the population varies around the average of its component pure lines. Starting with a population, one can sort out, by selection of parents, lines having desired characteristics. The practical breeder tends to do this in his selections of breeding stock and seeds. However, pure lines are stable only if cross-breeding is prevented, which

is frequently impossible. Selection within pure lines has been tested by many investigators. Experiments have been conducted on inheritance of size variation in different organisms, chemical content of potatoes

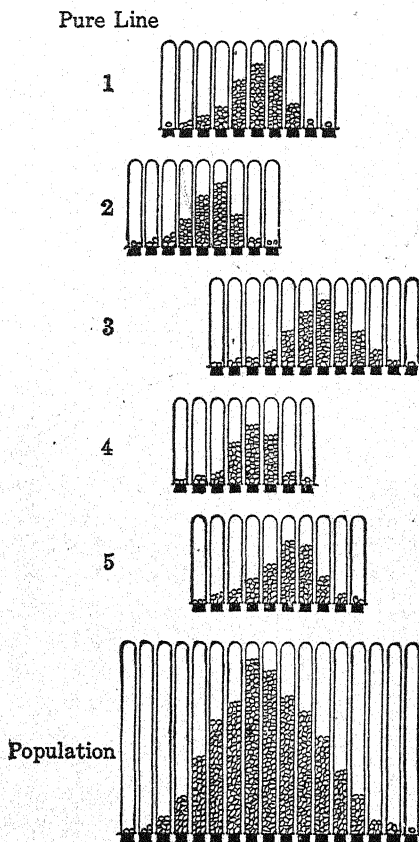


FIG. 102. Diagram illustrating the variations in weight of five pure lines of beans, and in the population formed when all are put together. Beans of the same weight are shown in the test tubes of each vertical line (cf. Fig. 520, p. 715, and Fig. 521, p. 716).

(After W. Johannsen, from H. E. Walter, "Genetics," copyright, 1922, by The Macmillan Co., reprinted by permission.)

and sugar-beets, egg-laying capacity in poultry, time of maturity of seeds, distribution of color in coats of mammals, and numerous other characteristics. In no case has selection shifted the average about which a pure line varies. Such variations, which are known as *fluctuations*, are conditioned by environmental effects during development and do not influence the characteristics of succeeding generations.

The Method of Experimental Breeding

Mendel's Contribution. Although the statistical or biometrical method gives a survey of the average course of heredity and variation in populations and pure lines consisting of numerous individuals, it is not of value in the analysis of individual cases. Experimental breeding in a controlled environment makes possible the accumulation of data on the process of heredity in all the individuals produced from

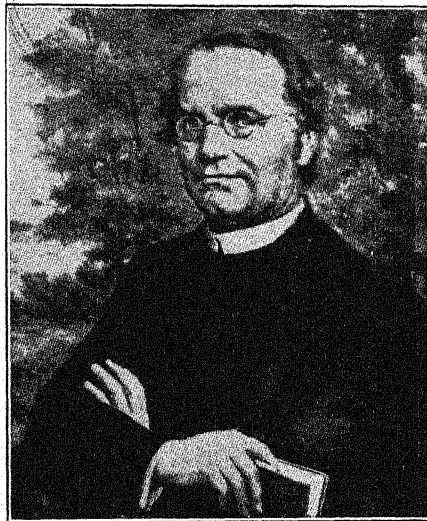


FIG. 103. Gregor Mendel.

(A portrait by Flatter from Jour. Heredity, 1940, vol. 31, reprinted by permission.)

generation to generation. The first recorded experiment in plant breeding was that of Camerarius in 1694. Not until Father Gregor Mendel (1822-1884) of the Augustinian Order carried out his careful work on the breeding of peas in the monastery garden at Brno (Brünn), Moravia, did this method yield results that revealed the principles of heredity (Fig. 103). Mendel's success came when he followed the inheritance of single specific characteristics in many individuals for many generations. One of his original experiments was cross-fertilization between peas with tall stems and those with dwarf stems. The use of parents that differ in one or more characteristics is known as the method of *hybridization*, and the offspring of such a cross-fertilization are *hybrids*. If the parents differ in one characteristic, such as length of stem in peas, a cross between them is called *monohybridization*.

Mendel found that without exception the offspring produced by hybridizing pure-bred tall and dwarf peas were tall, no matter which parent was tall and which dwarf (Fig. 104). When these hybrid tall

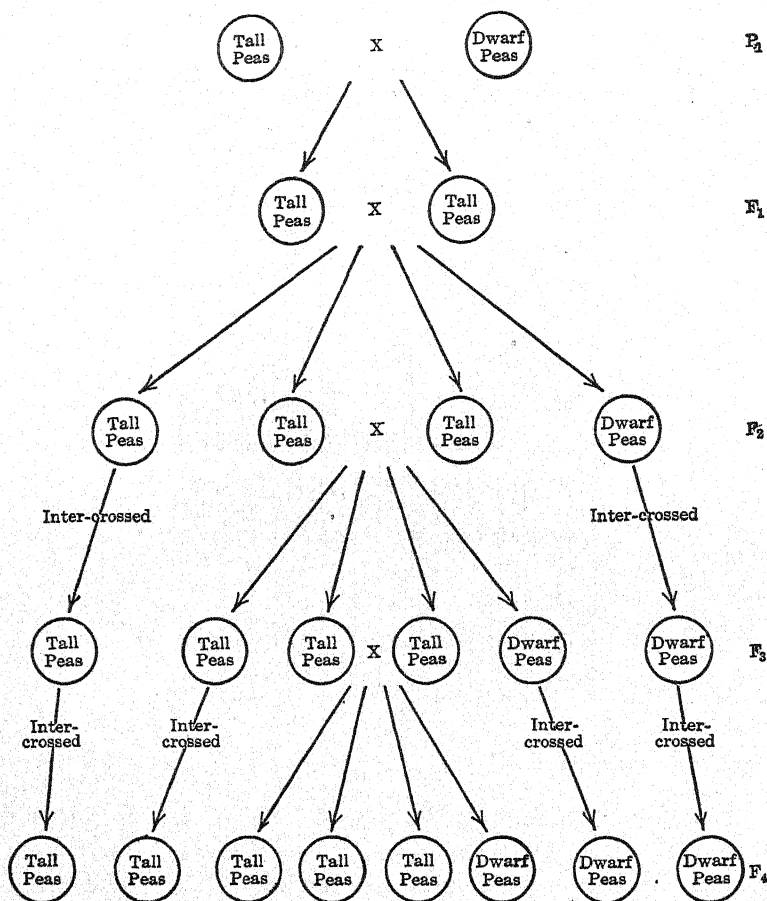


FIG. 104. Diagram to illustrate monohybridization in peas that differ in length of the stem; tall stem is dominant to dwarf stem.

peas were crossed among themselves, three-fourths of the next generation were tall like the tall parents, and one-fourth were dwarf like their dwarf grandparents. Dwarf stem, a characteristic which did not appear in the first filial generation (F_1 generation) that arose from the cross between tall and dwarf parents (P_1 generation), emerged unchanged in the second filial generation (F_2 generation). Dwarfness in such peas was as pure as was the dwarfness of their grandparents, and these F_2

dwarf peas gave rise only to dwarf peas when they were bred together. Breeding of the tall peas that constituted three-fourths of the F_2 generation revealed that, although these tall individuals superficially resembled one another, they were dissimilar as parents. One-third of the tall group gave rise in successive generations to tall offspring without exception. Such tall specimens, which constituted one-fourth of the total F_2 generation, corresponded in their resemblance to the pure-bred tall pea of the P_1 generation to that quarter of the group that was like the dwarf pea of the P_1 . The remaining two-thirds of the tall peas of the F_2 generation, or one-half of the offspring of the hybrid tall peas, were like their parents. When interbred, these F_2 tall peas gave rise to offspring in the ratio of three tall to one dwarf. As shown in Figure 104, this group again breaks up, when analyzed by breeding, into three types that occur in the ratio of 1:2:1; that is, one-fourth are pure tall peas, one-half hybrid tall peas, and one-fourth pure dwarf peas. In the case under discussion, tallness is said to be *dominant* to dwarfness; conversely, dwarfness is *recessive* to tallness.

It has been stated that the offspring of a cross between tall and dwarf peas are tall. Superficially, they cannot be distinguished from the tall parent. Yet these tall hybrids when bred together give some tall and some dwarf offspring. The tall peas of the F_2 generation are all similar in appearance; but experimental breeding proves that some reproduce only tall peas, whereas others are like their parents in giving rise to both tall and dwarf offspring. In such cases of inheritance with dominance, it is impossible to distinguish by superficial examination a hybrid individual from an individual that will breed true for the dominant character. Johannsen proposed the terms *phenotype*, to designate individuals that look alike, and *genotype*, to designate individuals that breed alike. The tall peas of the F_2 generation constitute a phenotype which can be shown to be made up of two genotypes. On the other hand, an individual that appears recessive will always breed true for the recessive characteristic; here the phenotype is identical with the genotype.

If any dominant characteristic be represented by D and any recessive characteristic by d , the following summary of the possible crosses can be made:

(Parents) $DD \times DD \rightarrow$ 100 per cent DD (offspring)

(Parents) $dd \times dd \rightarrow$ 100 per cent dd (offspring)

(Parents) $DD \times dd \rightarrow$ 100 per cent Dd (offspring)

(Parents) $Dd \times Dd \rightarrow$ 25 per cent DD plus 50 per cent Dd plus
25 per cent dd (offspring)

(Parents) $DD \times Dd \rightarrow$ 50 per cent DD plus 50 per cent Dd (offspring)

(Parents) $Dd \times dd \rightarrow$ 50 per cent Dd plus 50 per cent dd (offspring)

It must be understood that large numbers of specific cases were studied in order to obtain the percentages that have been indicated as characteristic of these crosses. Figure 105 gives some of the actual numbers of individuals in the F_2 generations in Mendel's original monohybridization experiments.

Character	Number of Dominants	Number of Recessives	Ratio
Form of seed	5,474 smooth	1,850 wrinkled	2.96 to 1
Color of seed coat	6,022 yellow	2,001 green	3.01 to 1
Length of stem	787 tall	277 dwarf	2.84 to 1
Color of flowers	705 colored	224 white	3.15 to 1
Position of flowers	651 axial	207 terminal	3.14 to 1
Form of pods	882 inflated	299 constricted	2.95 to 1
Color of unripe pods	428 green	152 yellow	2.82 to 1
Total	14,949	5,010	2.98 to 1

FIG. 105. Data from Mendel's original experiments, from which was derived the 3:1 ratio characteristic of the F_2 generation in monohybridization.

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Extension of Mendelian Theory. Mendel published the results of his studies in 1866, but they remained unknown until 1900, when his paper was discovered by three scientists who had independently reached the conclusions that he had stated so clearly. Since that time, his results have been confirmed by experiments with many plants and animals. For example, when a gray mouse is crossed with a white mouse, all the offspring are gray. This result indicates that gray coat-color is dominant to white coat-color in mice (Fig. 106). In the F_2 generation gray and white mice occur in the ratio of 3:1. Of the gray mice which constitute three-fourths of this F_2 generation, some are found to breed true for grayness, whereas others produce both gray and white offspring. Complete analysis by breeding reveals that 25

per cent of the F_2 generation are gray and will breed true for gray coat-color, 50 per cent appear gray but will not breed true, and 25 per cent are white and reproduce only white-coated individuals when interbred.

Up to this point the examples used have involved *inheritance with dominance*. Dominance and recessiveness do not, however, character-

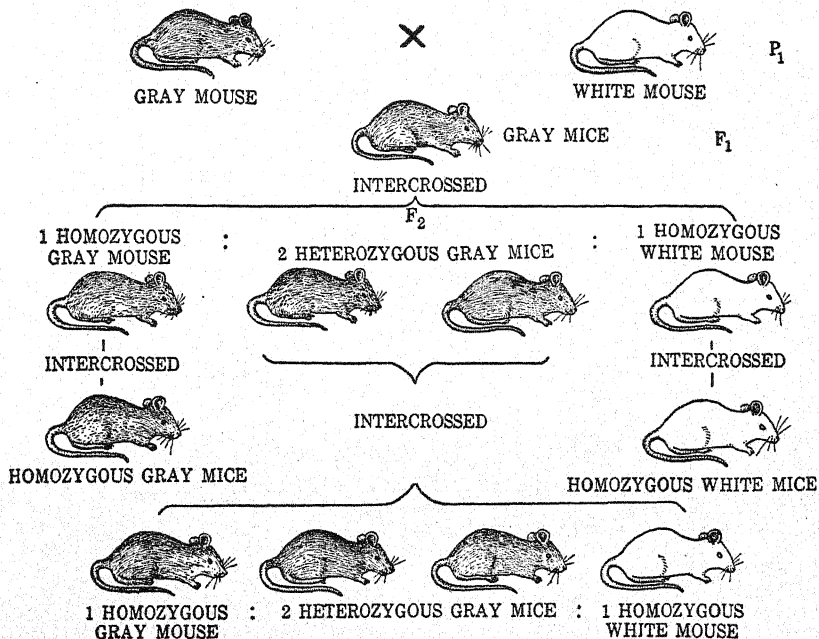


FIG. 106. Results of monohybridization of mice which differ in color of coat; gray coat-color is dominant to white coat-color (cf. Fig. 113, p. 177).

ize all cases of inheritance. If red and white four-o'clocks (*Mirabilis jalapa*) are crossed, the hybrids of the F_2 generation have pink flowers, not red or white. When these pink hybrids are interbred, offspring occur in the ratio of 1 red:2 pink:1 white. The individuals with red and white flowers breed true for these characteristic colors, whereas those with pink flowers always give three kinds of offspring in the typical 1:2:1 ratio. Another case of *inheritance without dominance* is the blue Andalusian fowl (Fig. 107). Blue Andalusian fowls are produced by crossing a type of black fowl with a certain kind of white fowl. They are, therefore, hybrids and, as would be anticipated, do not breed true. Blue Andalusian parents yield 25 per cent black chicks, 50 per cent blue chicks, and 25 per cent white chicks. The black and the white

offspring breed true, but the blue offspring, like all other blue Andalusians, will always yield 25 per cent black, 50 per cent blue, and 25 per cent white individuals. The course of inheritance for characteristics

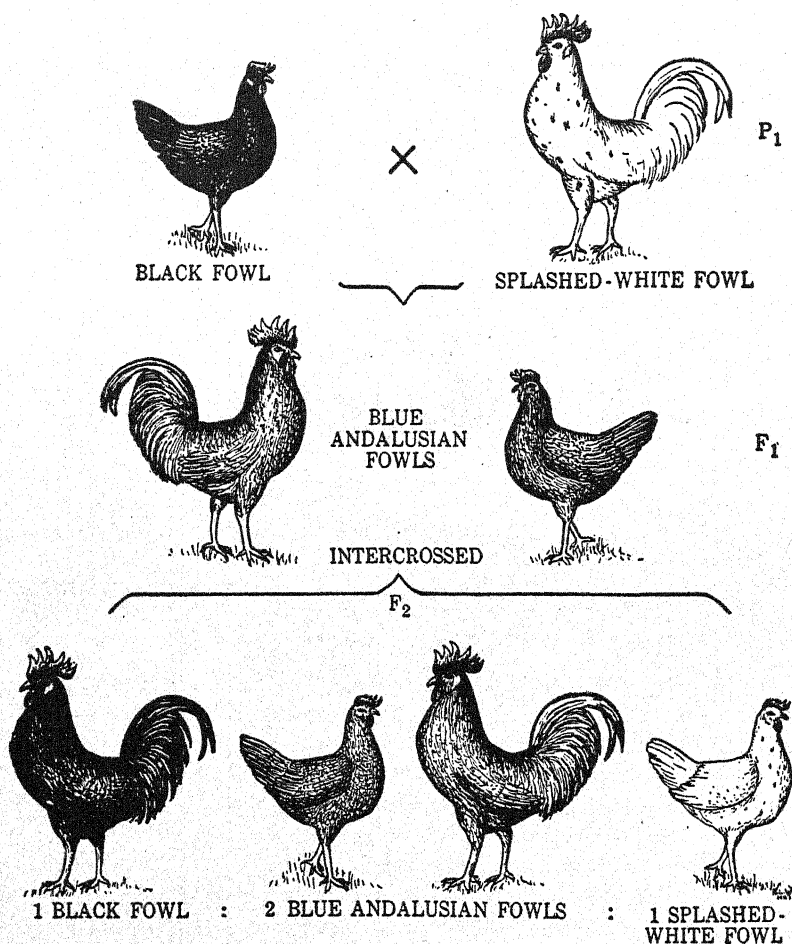


FIG. 107. Results of monohybridization of fowls which differ in color of feathers. This is an example of inheritance without dominance, since black and white parents yield blue hybrids. In the F_2 generation three visibly distinct types are produced in a 1:2:1 ratio.

that do not exhibit dominance is in no way different, therefore, from that for characteristics in which dominance occurs. In inheritance without dominance, the hybrid individuals, or those that will not breed true, can be distinguished superficially from those that will give rise to

offspring like themselves. Dominance is not an essential feature of heredity, although it is almost universally encountered in practical breeding. The behavior of the hereditary units in the germ cells is the same whether or not dominance is involved.

If two individuals that differ in two characteristics are crossed, the process is known as *dihybridization*. In guinea-pigs black hair and

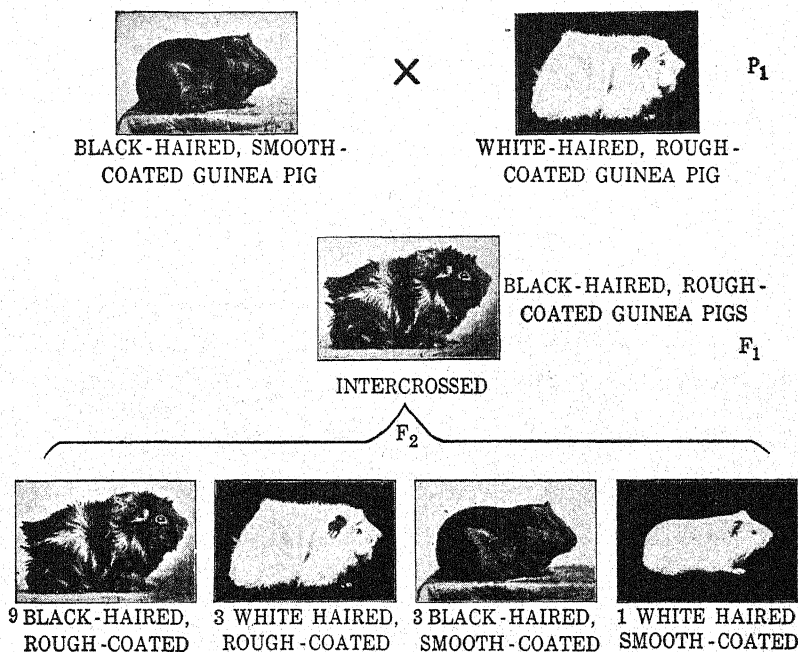


FIG. 108. Results of dihybridization in guinea-pigs which differ in color of hair and quality of coat; black hair is dominant to white hair, and rough coat to smooth coat (*cf.* Fig. 117, p. 182).

(Rearrangement of figures from W. E. Castle, "Genetics and eugenics," copyright, 1916, by Harvard University Press, printed by permission.)

rough coat are dominant to white hair and smooth coat. When a black-haired, smooth-coated guinea-pig is bred with a white-haired, rough-coated one, the offspring are all black-haired and rough-coated (Fig. 108). Whether these characteristics have been present in the male or in the female parent is not important; the combination always produces individuals in which both dominant characters are seen. When these F_1 hybrids are crossed, four kinds of offspring (phenotypes) result in the F_2 generation, in the following ratio—9 black-haired, rough-coated:3 white-haired, rough-coated:3 black-haired, smooth-coated:1 white-haired, smooth-coated. Mendel's original work on dihybrids

consisted in crossing wrinkled, green peas with smooth, yellow peas. The offspring of such a hybridization are smooth, yellow peas, a fact which indicates that smooth surface is dominant to wrinkled surface and yellow color is dominant to green color in the seeds. In the F_2 generation smooth, yellow peas, smooth, green peas, wrinkled, yellow peas, and wrinkled, green peas occur in the ratio of 9:3:3:1.

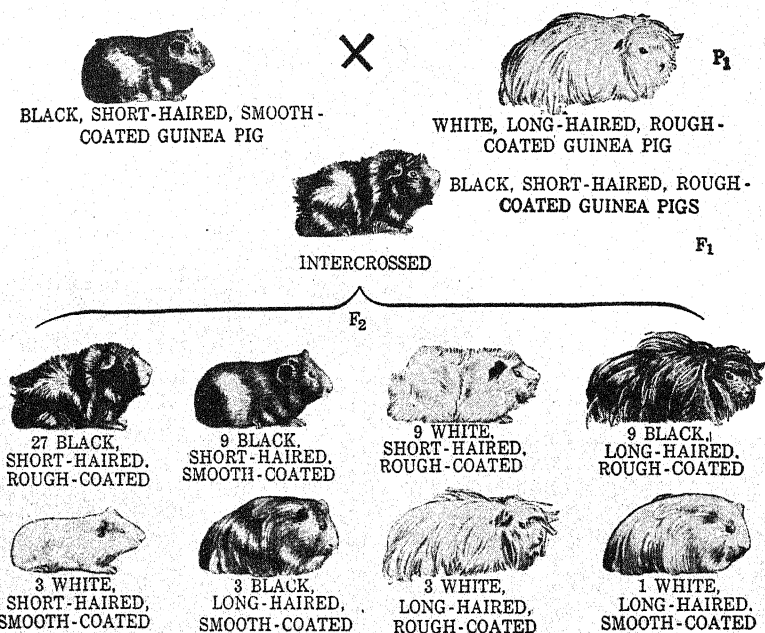


FIG. 109. Results of trihybridization in guinea-pigs which differ in color and length of hair and quality of coat; black hair is dominant to white hair, short hair to long hair, and rough coat to smooth coat.

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Trihybridization is the crossing of two individuals differing in three characteristics. A third character that can be used in guinea-pigs is length of hair, short hair being dominant to long hair. When a black, short-haired, smooth-coated guinea-pig is crossed with a white, long-haired, rough-coated guinea-pig, all the offspring of the F_1 generation are black, short-haired, and rough-coated (Fig. 109). Eight different kinds of individuals (phenotypes) are produced in the F_2 generation, in the ratio indicated—27 black, short-haired, rough-coated:9 black, short-haired, smooth-coated:9 white, short-haired, rough-coated:9 black, long-haired, rough-coated:3 white, short-haired,

smooth-coated:3 black, long-haired, smooth-coated:3 white, long-haired, rough-coated:1 white, long-haired, smooth-coated.

In the crosses previously considered, the sex of the parent having a particular characteristic has been of no significance. There are, however, cases of *sex-linked inheritance* in which the sex of the parent that possesses a certain character modifies its distribution in the offspring. Extensive work in experimental breeding for the study of

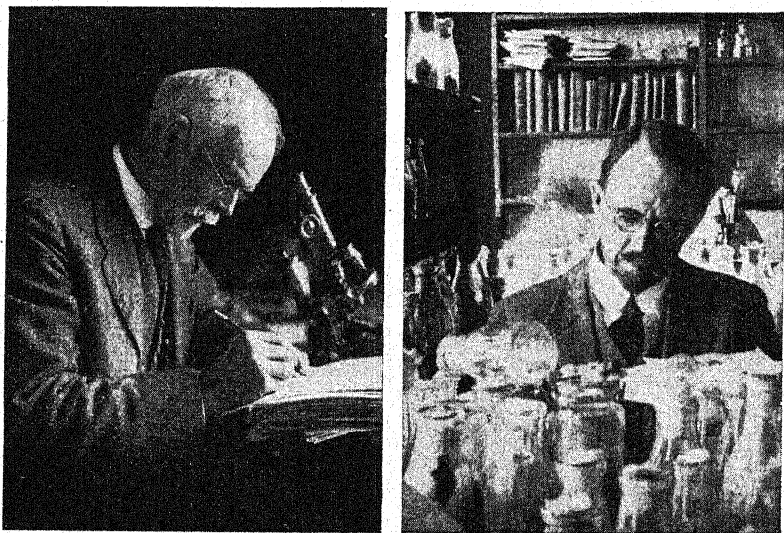


FIG. 110. *Left*, Edmund Beecher Wilson, 1856–1939. *Right*, Thomas Hunt Morgan, 1866–1945.

(Photographed by courtesy of A. F. Huettner.)

heredity and variation was first carried on in this country by T. H. Morgan and his students, who used the fruit-fly, *Drosophila* (Fig. 110). An example of sex-linked inheritance may be selected from the abundant data concerning heredity in this small insect. Red eye-color is dominant to white eye-color in *Drosophila* (Fig. 111). When a red-eyed female is crossed with a white-eyed male, both male and female offspring of the F_1 generation are red-eyed. If such red-eyed individuals are intercrossed, all the females and one-half the males of the F_2 generation have red eyes, whereas one-half the males have white eyes. The reciprocal cross, or the cross between a white-eyed female and a red-eyed male, gives very different results (Fig. 112). The males of the F_1 generation are white-eyed, and the females are red-eyed. In the F_2 generation red-eyed and white-eyed males and females occur in

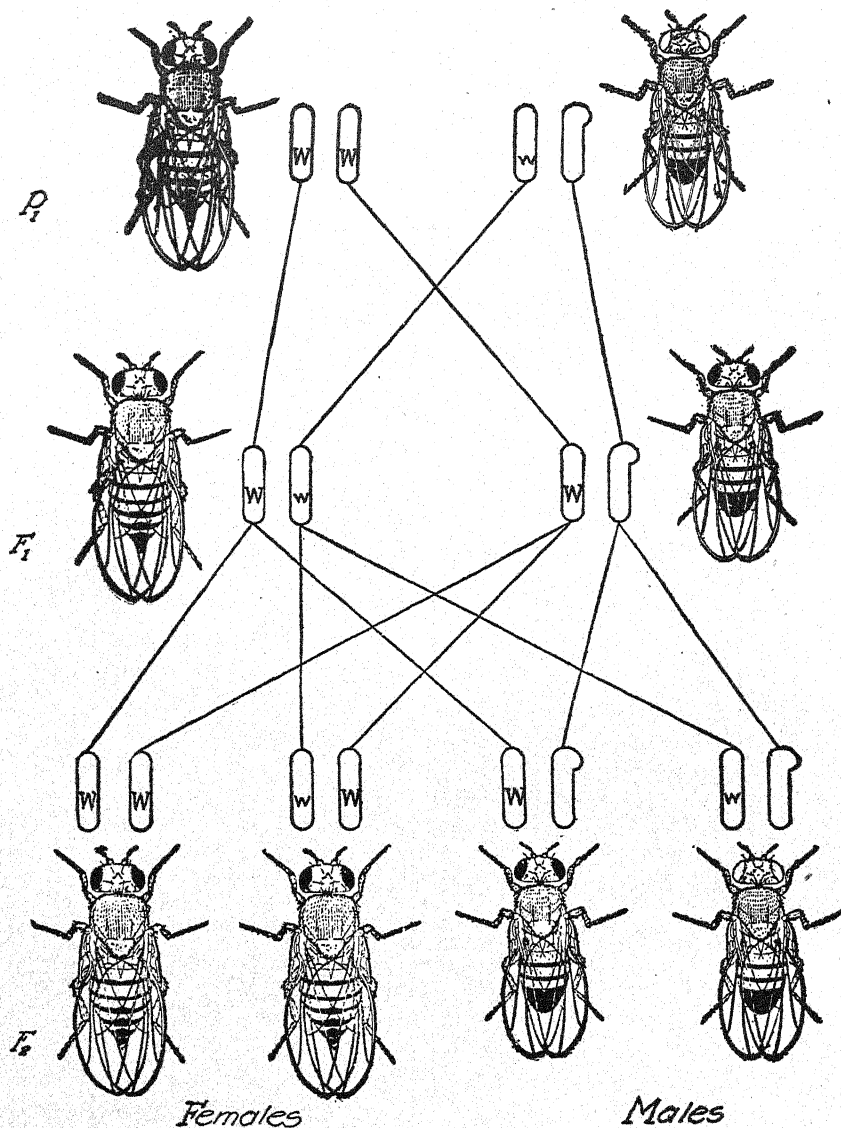


FIG. 111. Results of crossing a red-eyed female *Drosophila* with a white-eyed male. The X-chromosomes are represented as carriers of the genes determining eye-color; *W* is the symbol used for the gene for red eye-color which is dominant to the gene, indicated by *w*, for white eye-color (cf. Fig. 119, p. 184). The hook-shaped chromosome which does not contain a symbol for a gene represents the Y-chromosome of the male (cf. p. 204). This cross is the reciprocal of that shown in Fig. 112.

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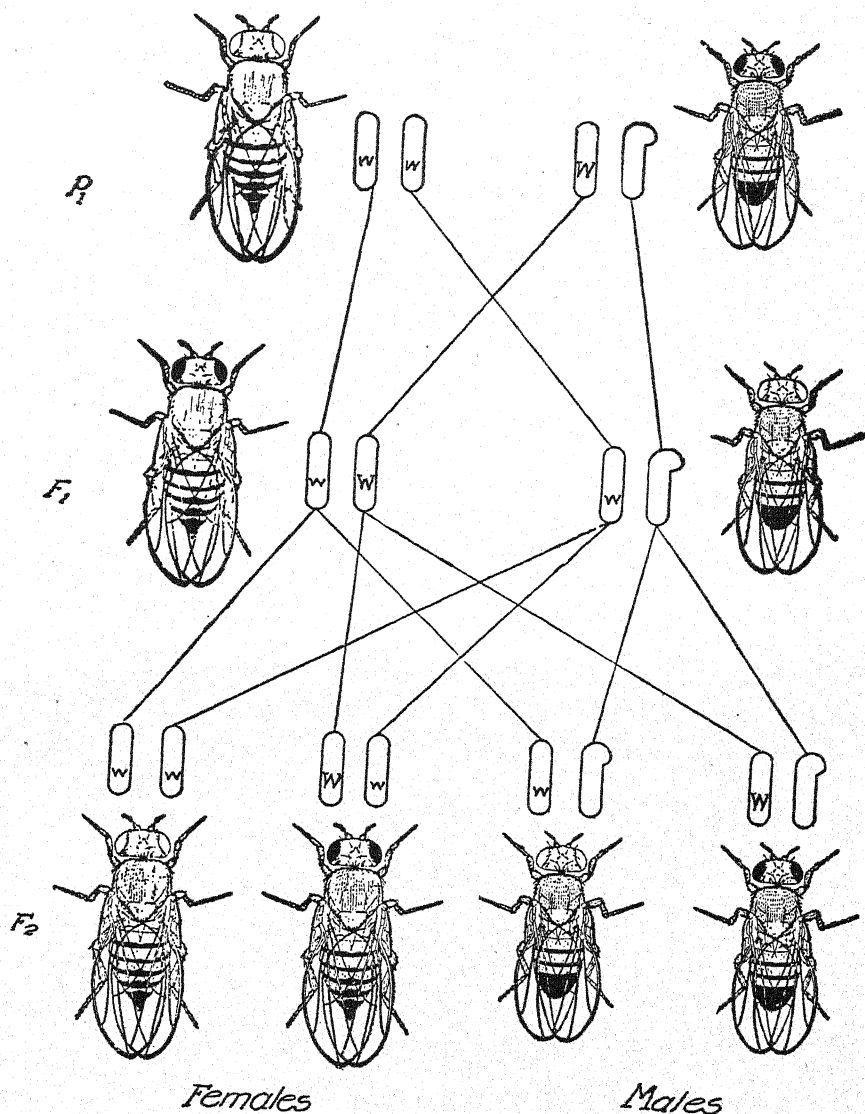


FIG. 112. Results of crossing a white-eyed female *Drosophila* with a red-eyed male (cf. Fig. 120, p. 185). The X-chromosomes and the symbols for the genes are explained in the legend of Fig. 111, which shows the reciprocal of this cross.

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equal numbers. When the mechanism of inheritance is considered in the following section, sex-linked inheritance will be found to furnish additional confirmation of Mendelian principles.

The method of experimental breeding, first carefully used by Mendel, has yielded a vast amount of detailed information concerning the course of inheritance of specific characteristics by particular individuals through many successive generations. It was clear to Mendel that the reproductive cells, which do not, of course, exhibit the characters of stems and seeds, must carry something correlated with the appearance of characters of the adult organism from generation to generation. These "somethings" are usually called *hereditary factors*, or *genes*. Mendel proved that a factor related to a specific expression of a character, such as dwarf stem, was not altered by association with a factor for the alternate expression of that character, such as long stem. Hereditary factors for the alternate or allelomorphic states in which characters are found to exist retain their unmodified independence even when present together in the cells of a hybrid individual and even though one factor is without effect in the presence of the other. When a hybrid produces its reproductive cells, these two *allelomorphic factors*, or *alleles*, one for each of the visible expressions of the character under consideration, must be able to separate, or *segregate*, from one another and occur alone in different reproductive cells. When they combine at random to form individuals of the next generation, new combinations of genes occur which condition the characteristic ratios of mono-, di-, and trihybridization experiments. The details of the behavior of the genes can be understood best if considered in connection with that of the chromosomes.

The Method of Cytology

Chromosomes as Carriers of the Genes. When Mendel's work was brought to light in 1900, it was well known that new individuals developed from zygotes formed by the union of ova and spermatozoa. These gametes, or mature germ cells, carry the haploid number of chromosomes that is characteristic of the species; the diploid number is restored in the zygote (*cf.* pp. 116 and 132). As the zygote divides and mitosis occurs, the chromosomes are distributed equally to all the cells of the new individual (*cf.* p. 113). The primordial germ cells of any individual contain chromosomes that can be grouped in pairs of similar size and shape. One member of each pair is of paternal and the other of maternal origin (*cf.* Fig. 63, p. 115). When the first meiotic division occurs, homologous chromosomes disjoin and pass into

different cells. This disjunction does not involve the separation of the sets of chromosomes that came from the two parents at the time of fertilization. On the contrary, the distribution of homologous chromosomes is random, with the members of each pair of chromosomes separating independently. These facts were discovered by the micro-

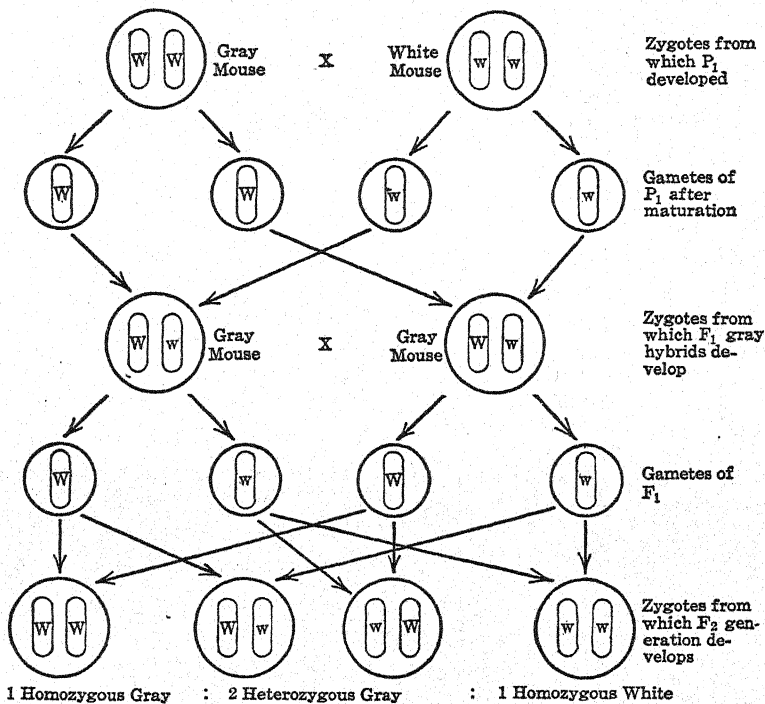


FIG. 113. A cross between a homozygous gray mouse and a homozygous white mouse (*cf.* Fig. 106, p. 169). The diagram illustrates the segregation of a pair of genes when their carriers, a pair of homologous chromosomes, undergo disjunction; notice the possible combinations that can occur between gametes.

W, gene for gray coat-color; w, gene for white coat-color.

scopical examination of germ cells by the methods of cytology. In 1902 W. S. Sutton called attention to the behavior of the chromosomes as furnishing a cellular mechanism for the explanation of Mendel's results. Since that time the theory of the chromosomes as carriers of the genes has been greatly extended, and chromosomes are now considered to be the physical basis of heredity. The researches of E. B. Wilson (Fig. 110) and Nettie M. Stevens in 1905-1906 were important in the analysis of the numbers and types of chromosomes in male and female animals; the work of Eleanor E. Carothers in 1917 furnished evidence

of the independent assortment of homologous chromosomes during the meiotic divisions.

If the example of monohybridism between a gray and a white mouse is analyzed according to the conception that the genes are located in the chromosomes, the assumption is made that the zygote from which the gray mouse developed contained two genes for grayness,

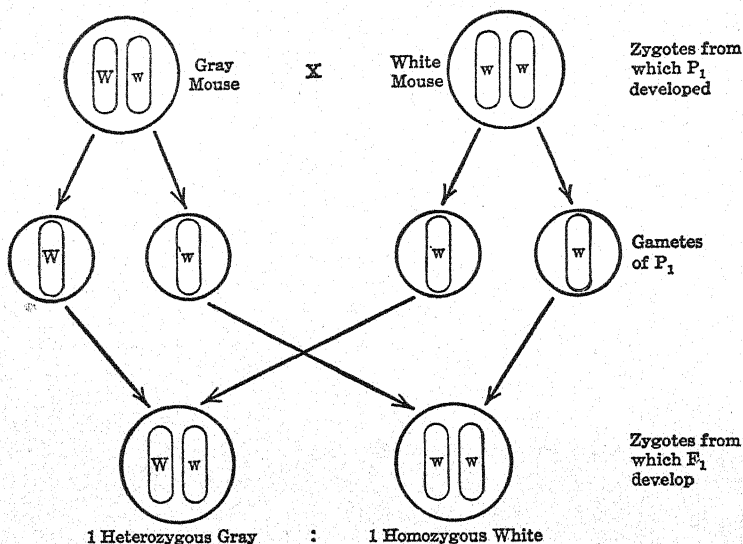


FIG. 114. A cross between a heterozygous gray mouse and a homozygous white mouse. The diagram illustrates the segregation of a pair of genes when their carriers, a pair of homologous chromosomes, undergo disjunction; notice the possible combinations that can occur between gametes. *W*, gene for gray coat-color; *w*, gene for white coat-color.

one from each of its parents, whereas the zygote from which the white mouse developed contained two genes for whiteness, one from each of its parents (Fig. 113). Each of these genes is regarded as being located in a separate chromosome, but the two genes of each animal are resident in homologous chromosomes. When separation of the homologous chromosomes occurs at the disjunctive division during meiosis, the genes are carried into different gametes. All the gametes of the gray parent possess a single gene for gray coat-color, and those of the white parent a single gene for white coat-color. When fertilization occurs, each zygote obtains two genes for coat-color, but one is for whiteness and one for grayness; the allelomorphic genes are now together in the same zygote. A zygote of this kind is called a *heterozygote*, in contrast to the zygotes like those from which the parents

developed, which are known as *homozygotes* because the genes of the pair are alike. The F_1 individuals are spoken of as *heterozygous*, and the parents in this case are called *homozygous*. As can be seen from Figure 113, two kinds of gametes are formed when disjunction occurs in individuals of the F_1 generation, and three kinds of combinations of gametes with chromosomes and genes are possible in the F_2 genera-

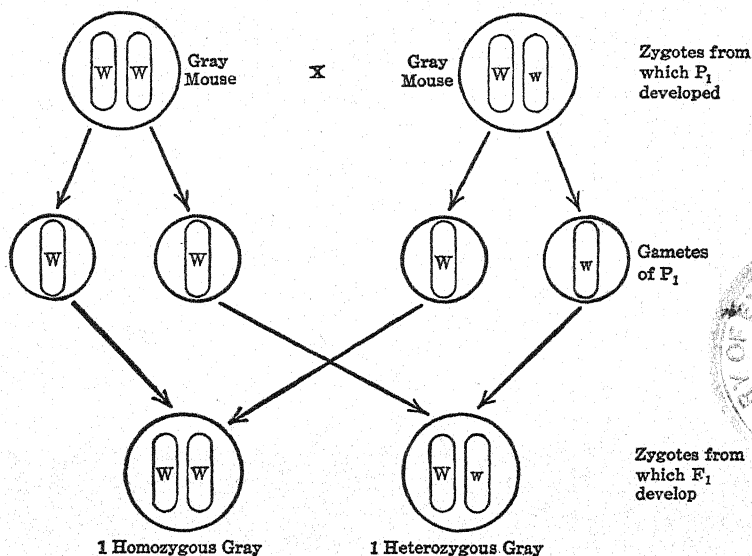


FIG. 115. A cross between a homozygous gray mouse and a heterozygous gray mouse. The diagram illustrates the segregation of a pair of genes when their carriers, a pair of homologous chromosomes, undergo disjunction; notice the possible combinations that can occur between gametes. *W*, gene for gray coat-color; *w*, gene for white coat-color.

tion. According to chance, one of these classes, the *Ww* combination, will occur twice as frequently as either the *WW* or the *ww*. The effect of the dominance of the gene for grayness is such that both homozygous and heterozygous gray mice look alike, and the apparent ratio in the F_2 generation is 3 gray:1 white. It is necessary, therefore, to obtain offspring from particular crosses in order to differentiate genetically between individuals that exhibit a dominant characteristic, that is, to separate the genotypes of the dominant phenotype. The theoretical explanation of the results obtained when a heterozygous gray mouse is crossed with a white mouse, which will always be homozygous since white is recessive, is presented in Figure 114. This is known as a *back-cross with a recessive*. The difference between

the offspring obtained in this cross and those obtained by crossing a homozygous gray with a white mouse furnishes the type of breeding test used for differentiating homozygous from heterozygous dominant individuals (Fig. 113). The diagram in Figure 115 shows why indiscriminate crossing between the gray mice would fail to yield information that would enable one to distinguish homozygous gray mice with certainty. In the case illustrated all the offspring will be gray in both the F_1 and F_2 generations; the same situation would prevail if both original gray mice had been homozygous. However, if any white mice appeared in a cross between two grays, their presence would prove both parents to be heterozygous.

The breeding results are explained adequately in these cases of monohybridism by the assumption that the allelomorphic genes conditioning the alternate expressions of the character used are carried in homologous chromosomes and so distributed to gametes and zygotes (Fig. 116). The theory of the chromosomes as the physical basis of heredity can likewise be used to explain cases of di- and trihybridism. In *Drosophila* long wing (V) is dominant to short or vestigial wing (v), and gray body-color (E) is dominant to ebony (e) body-color. A fly with vestigial wings and gray body ($vvEE$) is mated with a long-winged fly with ebony body ($VVee$) (Fig. 117). At the time of the first meiotic division the homologous chromosomes of each pair undergo disjunction and pass into different gametes. The gametes produced by the parents contain genes vE and Ve , respectively. The zygotes of the F_1 generation will be $VvEe$ and will develop into long-winged, gray-bodied flies. Four different kinds of gametes can be formed by these F_1 individuals, since the different pairs of homologous chromosomes assort independently when they undergo disjunction at the first meiotic division. *Segregation* and *independent assortment* of genes yield the following four classes of gametes in any F_1 individual: VE , Ve , vE , and ve . Random combination of gametes containing such genes gives rise to sixteen possible zygotes that develop into the F_2 generation as shown in the checkerboard at the bottom of Figure 117. There are four phenotypes occurring in a 9:3:3:1 ratio and nine genotypes ($VVEE$, $VVEe$, $VvEE$, $VvEe$, $VVee$, $Vvee$, $vvEE$, $vvEe$, and $vvee$).

Linkage. The discussion of the chromosomes as the carriers of the genes has been concerned so far with what could occur if each gene were carried in a separate chromosome. It was discovered by W. Bateson and R. C. Punnett in 1906 that certain characteristics were linked in inheritance. They found, in crossing a sweet pea with purple flowers and long pollen grains and a sweet pea with red flowers and

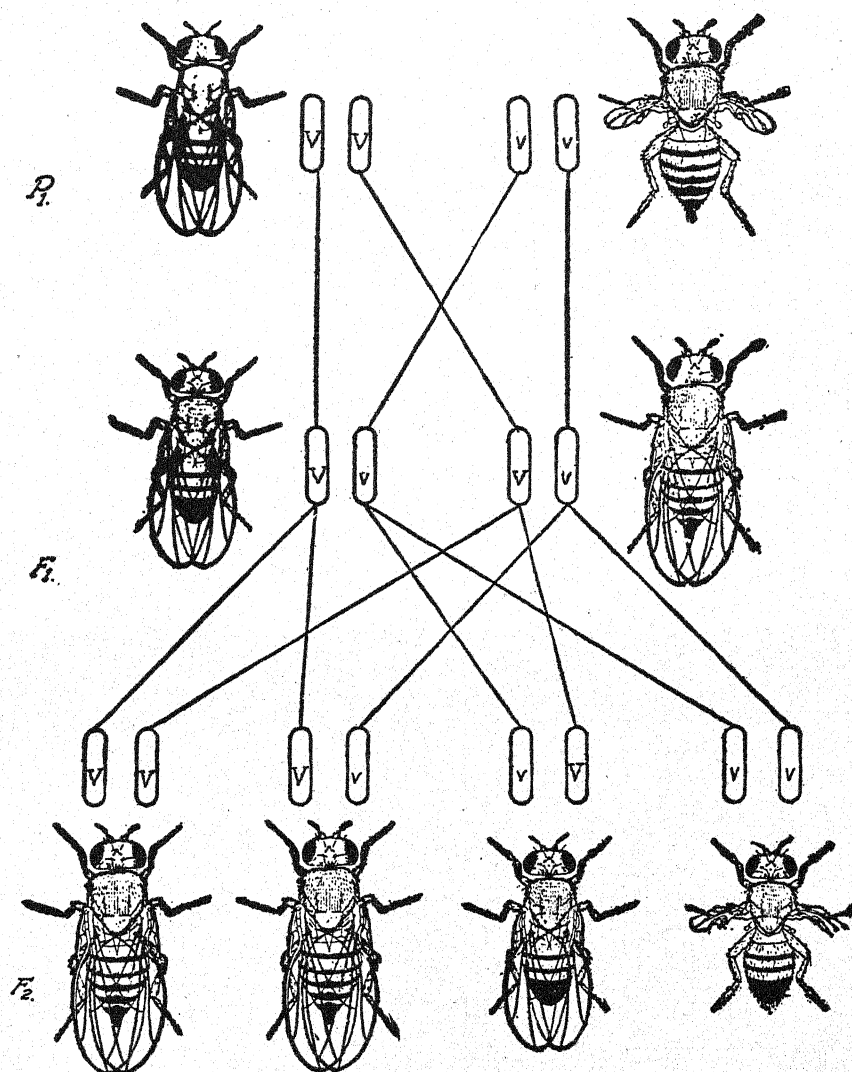


FIG. 116. Results of monohybridization of flies which differ in type of wing. The chromosomes are shown as the carriers of the genes; *V* is the symbol used for the gene for long wing, which is dominant to the gene, *v*, for vestigial wing (cf. Fig. 113, p. 177).

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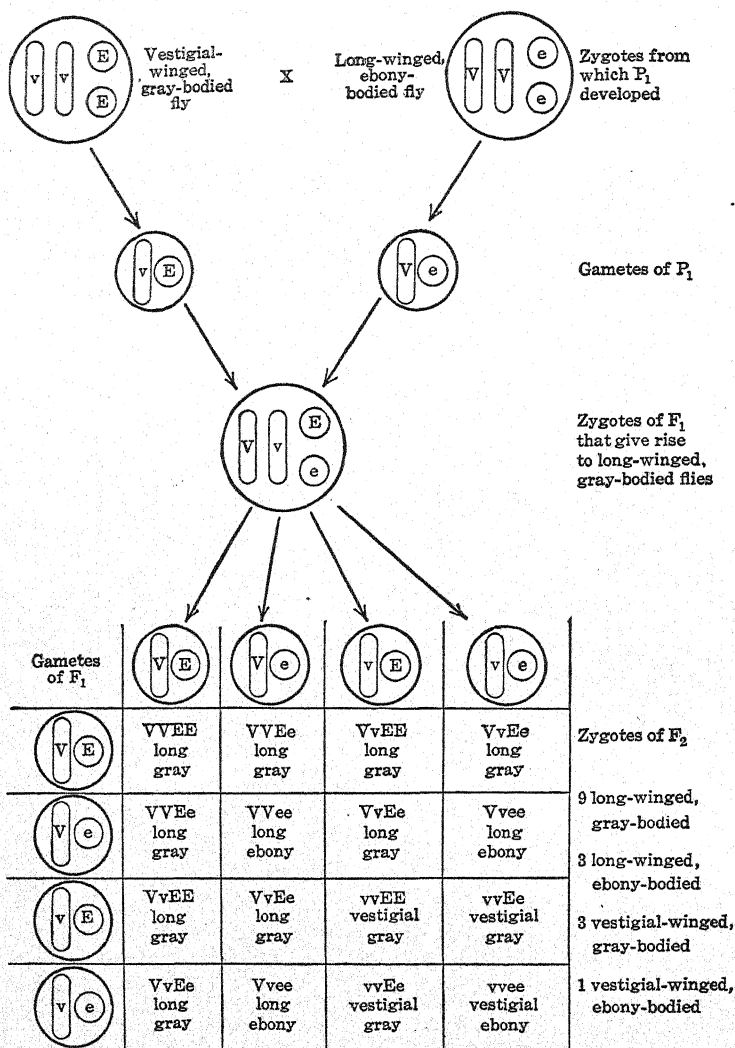


FIG. 117. A case of dihybridization between a vestigial-winged, gray-bodied fly (*Drosophila*) and a long-winged, ebony-bodied fly (cf. Fig. 108, p. 171). The diagram illustrates disjunction and independent assortment of two pairs of homologous chromosomes which carry two pairs of genes; notice the possible combinations that can occur between the gametes formed. *E*, gene for gray body; *e*, gene for ebony body; *V*, gene for long wing; *v*, gene for vestigial wing.

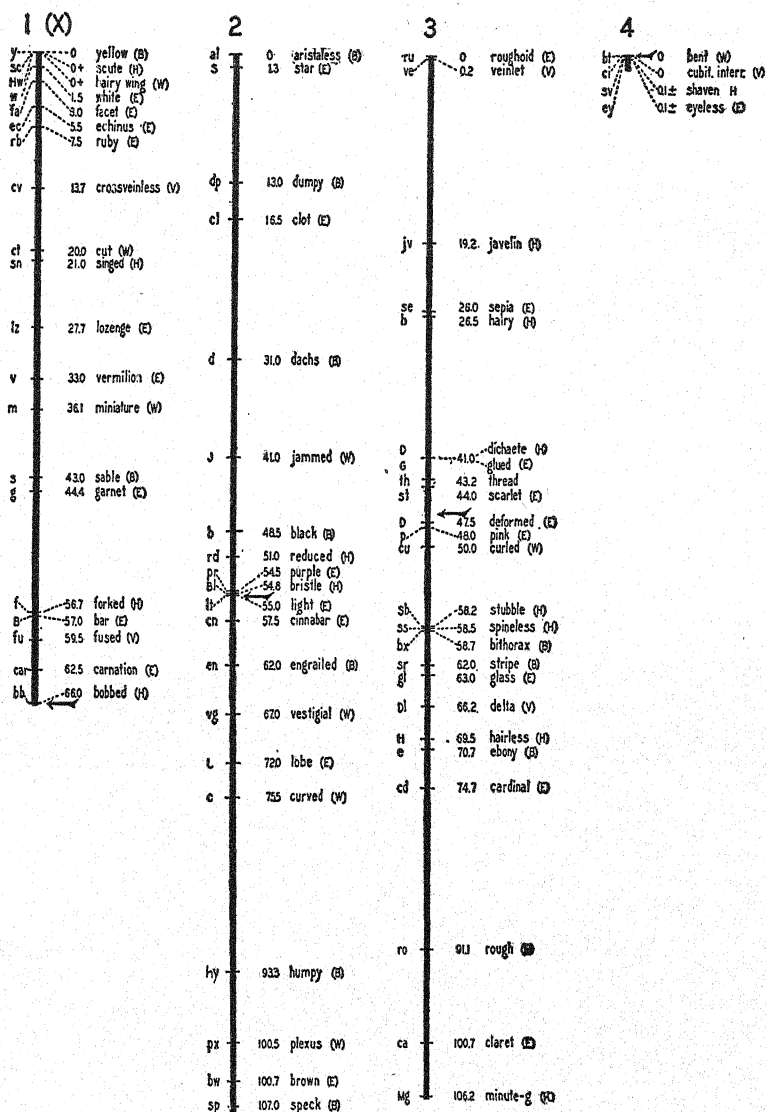


FIG. 118. Maps of the four chromosomes of the haploid set in *Drosophila*; the genes located in any one chromosome and their allelomorphs constitute a linkage group. Chromosome 1 is the X-chromosome, and 4 is the small round one (cf. Fig. 60, p. 111, and Fig. 121 A). Letters in parentheses indicate part of fly where effect of mutant gene is observed: B, body; E, eyes; H, bristles; V, venation of wings; W, wings. The positions of association with the spindle (cf. p. 110) are indicated by arrows.

(After Bridges, from A. H. Sturtevant and G. W. Beadle, "An introduction to genetics," copyright, 1939, by W. B. Saunders Co., reprinted by permission.)

round pollen grains, that the genes which came from each parent tended to remain together instead of assorting independently during meiosis. The study of inheritance of some four hundred genes in *Drosophila* shows that they fall into four groups; the genes composing each of these groups are said to be *linked* (Fig. 118). Cytological investiga-

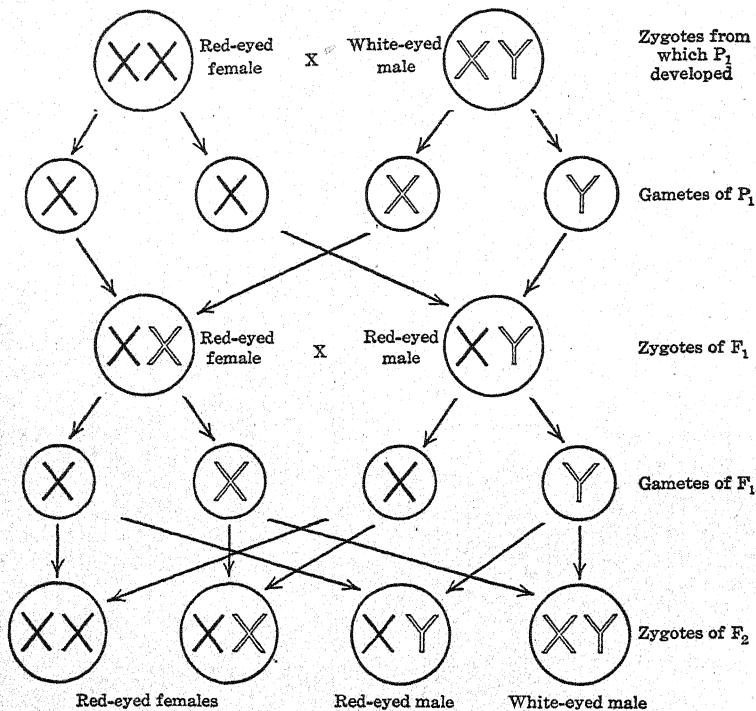


FIG. 119. A cross between a red-eyed female *Drosophila* and a white-eyed male (cf. Fig. 111, p. 174). The diagram illustrates disjunction of sex chromosomes during the formation of gametes and the possible combinations of these; the X-chromosomes carry genes for eye-color. This is the reciprocal of the cross shown in Fig. 120. \times , X-chromosome carrying gene for red eye-color; \bar{x} , X-chromosome carrying gene for white eye-color; Y , Y-chromosome which is confined to males and does not carry a gene for eye-color.

tion demonstrates the presence of four pairs of chromosomes in *Drosophila* (cf. Fig. 60, p. 111), and pairs of linked genes are known to be carried by pairs of homologous chromosomes. Furthermore, there is evidence which is interpreted to indicate that genes in a chromosome are arranged like beads on a string, and relative distances between genes in the string have been computed (Fig. 118). This *linear*

order of the genes makes the longitudinal doubling of the chromosomes with consequent separation of the chromonemata during mitosis significant as a qualitative division (*cf.* p. 113).

The example of sex-linked inheritance described as a breeding experiment (p. 173) can be explained if it be assumed that the X-

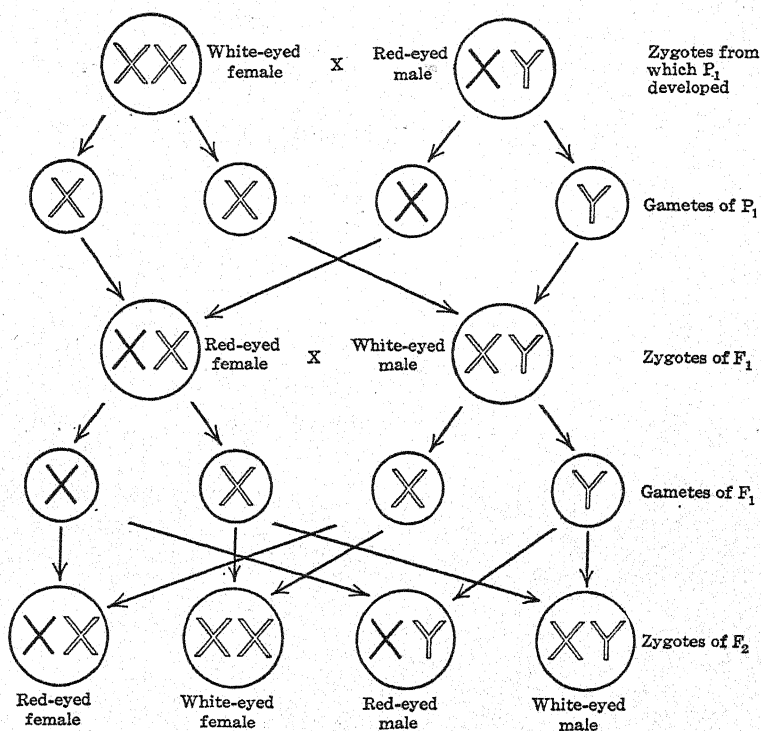


FIG. 120. A cross between a white-eyed female *Drosophila* and a red-eyed male (*cf.* Fig. 112, p. 175). The diagram illustrates disjunction of sex chromosomes during the formation of gametes and the possible combinations of these; the X-chromosomes carry genes for eye-color. This is the reciprocal of the cross shown in Fig. 119, the legend of which describes the symbols.

chromosomes carry the genes concerned with red and white eye-color. It will be recalled that in the cells of a female there are two so-called X-chromosomes, whereas in the male only one X-chromosome is found (*cf.* Fig. 60, p. 111). The male *Drosophila* possesses one X-chromosome and a Y-chromosome which carries very few genes and does not leave the male line. Each ovum formed during maturation contains one X-chromosome; one-half of the sperm have an X-chromosome, the other half have a Y-chromosome. In the cross between a homo-

zygous red-eyed female *Drosophila* and a white-eyed male each ovum contains an X-chromosome carrying a gene for red eye-color, whereas half the sperm have an X-chromosome bearing a gene for white eye-color and half have a Y-chromosome which has no gene for eye-color (Fig. 119). Random unions of ova and spermatozoa result in red-eyed females and red-eyed males in the F_1 generation. The females are red-

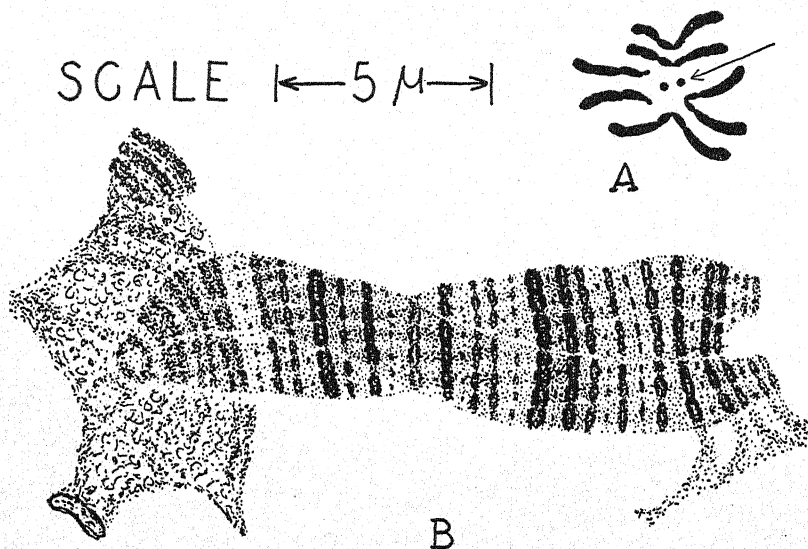


FIG. 121. Chromosomes of *Drosophila*. A, equatorial plate from an oögonium; chromosome pair IV is seen in the center of the group. B, chromosome pair IV from a salivary gland cell; members of each pair of chromosomes are closely associated, greatly increased in size, and exhibit conspicuous banding.

(From C. B. Bridges, 1935, Jour. of Heredity, vol. 26.)

eyed because the gene for red eye-color is dominant to the gene for white eye-color. These females are, however, heterozygous for eye-color and give rise to two kinds of ova, in one of which the X-chromosome carries a gene for red eye-color, and in the other the X-chromosome carries a gene for white eye-color. Half the spermatozoa produced by the red-eyed males have an X-chromosome with a gene for red eye-color and half have the Y-chromosome. Combinations of the gametes in a cross between a male and a female of the F_1 generation result in red-eyed females, red-eyed males, and white-eyed males. In this kind of inheritance the white-eyed characteristic of the male parent does not occur in the F_1 generation but reappears in one-half the males of the F_2 generation. The reciprocal cross, in which a white-

eyed female is mated with a red-eyed male, is shown in Figure 120. If the distribution of the X-chromosomes is followed, the reason for the difference between the offspring from these two crosses should be clear. It is to be understood that sex linkage is not an exception to the Mendelian principles but confirms the theory that the chromosomes carry the genes.

Cytology has furnished knowledge of the behavior of chromosomes and their transmission from one generation to the next. The experi-

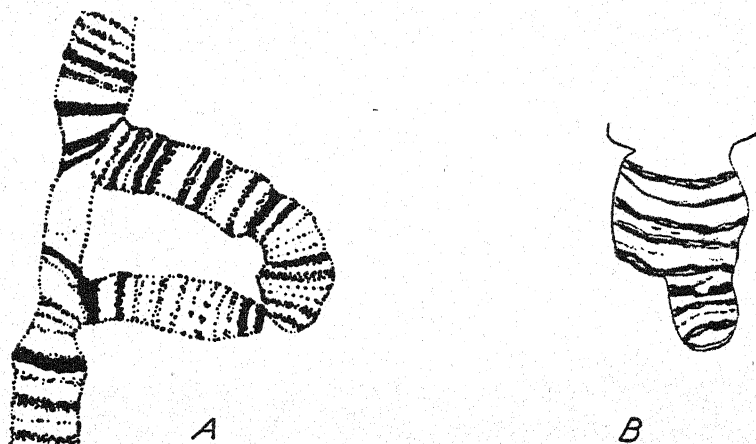


FIG. 122. Chromosomal aberrations seen in the paired salivary-gland chromosomes of *Drosophila*. A, part of the pair of X-chromosomes, one of which has lost an internal section by deletion (cf. Fig. 127, p. 196); the bent portion of the normal partner indicates the length of the deleted section. B, the end of a pair of X-chromosomes, one of which has lost a terminal section.

(A, from T. S. Painter, 1934, *Jour. of Heredity*, vol. 25; B, from M. Demerec and Margaret E. Hoover, 1936, *Jour. of Heredity*, vol. 27.)

mental breeder has been able to explain adequately the results obtained in his breeding experiments by the assumption that what is present in the zygote and determines the appearance of a character in an adult organism is carried by the chromosomes. These hypothetical determiners of inherited characters are known as hereditary factors, or genes. It is known that many genes are found in a single chromosome and that they are arranged in a row along the length of the gene-string, which may be the chromonema. In the cells of the salivary gland of *Drosophila* the chromosomes are very large because of several reduplications of the chromonemata without nuclear division (Fig. 121). The bands on these chromosomes are characteristic and constant in position on the members of a pair which are closely associated

side by side. When certain genes are found to be missing in breeding experiments, a cytological examination of these banded chromosomes reveals that certain bands are absent (Fig. 122); that is, the genes of a linkage group can be considered to occupy definite positions on a pair of homologous chromosomes.

Genes are distributed equally by the mechanism of mitosis to all the cells derived from a zygote. The mechanism of disjunction and independent assortment of the pairs of homologous chromosomes during maturation of the germ cells, and the possibilities of random combination of the germ cells, furnish a cellular basis by means of which Mendelian ratios can be explained.

The Method of Experimental Embryology

Experimental breeding is usually carried on under the conditions most favorable for the organisms concerned. The results obtained, therefore, are comparable with what might be expected to occur in uncontrolled breeding in the natural habitat. This normal course of inheritance can be observed and interpreted, as has been explained. From it we learn the laws of the transmission of the hereditary units; we learn the mechanism of heredity.

How does the particular complement of genes in a zygote influence the course of development in such a way as to condition the appearance of the phenotype? What is the relation of gene to character? In this, as in many fields of study, a knowledge of what happens under abnormal or unusual conditions may clarify our understanding of the normal situation. In the examples cited to illustrate Mendelian principles, a certain combination of genes always gives a certain type of individual. However, if the environment is changed and the genetic combination remains the same, the individuals may be different (*cf.* p. 158). For example, the red primrose has red flowers if kept at a temperature ranging from 15° to 20° C. A plant with the same genes but reared at a temperature of 30° to 35° C., with other environmental conditions unchanged, produces white flowers. If a plant with white flowers is brought into a room at 15° to 20° C., the flowers that develop later will be red. The effect of the genes for color of flower is limited by the temperature of the environment in which the flowers develop. That the gene is not altered is shown by the ability of the plant to cease producing white flowers and give rise to red ones when kept at a different temperature. The same type of effect has been demonstrated in *Drosophila*. A certain race of the fruit-fly is distinguished from the normal by the fact that there are very few

black bands on the abdomen. When this race is reared on a rich supply of moist food, the abdominal bands are almost completely absent in all individuals. The same stock raised on scant, dry food exhibits normal banding of the abdomen. If a culture is started with abundant moist food which is not replenished but allowed to become dry, the individuals that develop first will show abnormal banding, and those that develop later will appear normal. These flies are genetically the same; the difference in their appearance is conditioned by the environment in which they develop. In other words, the appearance of characters in an adult individual is dependent on the presence of certain genes in the zygote acting in a particular environment during development.

The age of an individual sometimes affects the development of characters. Certain characters may not appear until the individual reaches a particular age. In other cases a character may appear in early stages of development and be lacking in the adult. Age is, in this sense, a phase of the environment. The relationship between genes and environment is shown further by the fact that in *Drosophila* red color is confined to the eyes and does not occur on the legs or wings. The mechanism of mitosis makes it reasonable to suppose that all genes are distributed equally to all cells. Yet these genes are effective in determining red color, for example, only in restricted regions of the organism. The influence of genes is likewise dependent upon their association with certain other genes; evidence for the interaction of genes is clear-cut but very complicated and will not be given here. At least twenty-five pairs of allelomorphic genes are concerned with eye-color. Conversely, a single pair of genes may influence more than one character. In *Drosophila* the genes for rudimentary wings affect characters of the legs and the number of eggs laid.

Genes are the hypothetical units that determine inheritance in organisms. At least two allelomorphic genes are responsible for the appearance of each character of the individual. In many instances it is known that three or more allelic states of the gene for a particular character exist. No more than two of these *multiple allelomorphs* are present in a particular individual. There may be many pairs of allelomorphic genes that interact to produce a given character. A single pair of genes may also influence the appearance of more than one character. Certain environmental factors during development of a character limit the effect of the genes. The tentative hypothesis concerning the nature of genes proposes that they are chemical compounds; more definite knowledge awaits additional information con-

cerning the physico-chemical nature of the chromosomes of which the genes are a part.

Investigations of the way in which genes in the nuclei of the cells of an organism actually influence its development have recently become possible. The data indicate that a particular allele is necessary



FIG. 123. Inheritance of hands and feet having only one digit. The two children, one of whom has normal hands and feet, are held by their mothers, who are daughters of the woman at the right. A dominant gene conditions this malformation; that is, individuals who show the trait may be either homozygous or heterozygous. Normal individuals are homozygous for the recessive allele, and the deformity does not appear in their offspring. A marriage between a heterozygous deformed person and a normal person gives normal and defective progeny in a 1:1 ratio. This particular type of hereditary skeletal deformity has been found only in an isolated Hindu community

(From R. M. Hegdekatti, 1939, *Jour. Heredity*, vol. 30, reprinted by permission.)

for the production of a particular enzyme which must be present :
the character known to be conditioned by the allele appears. Lon
chain reactions occurring between the constituents of the cytoplasm i
any particular region, set off by one genic enzyme and probab'
modified by many others, are thought to result in the differentiati
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Human Inheritance

Man's characteristics are inherited from generation to generation, as are those of other living organisms. The course of heredity is well understood in many cases, and much information has been accumulated (Figs. 123, 124, and 125). For the inheritance of human eye-color there is a pair of genes, the dominant member of which must be present if any pigment is to be deposited in the eye. Individuals

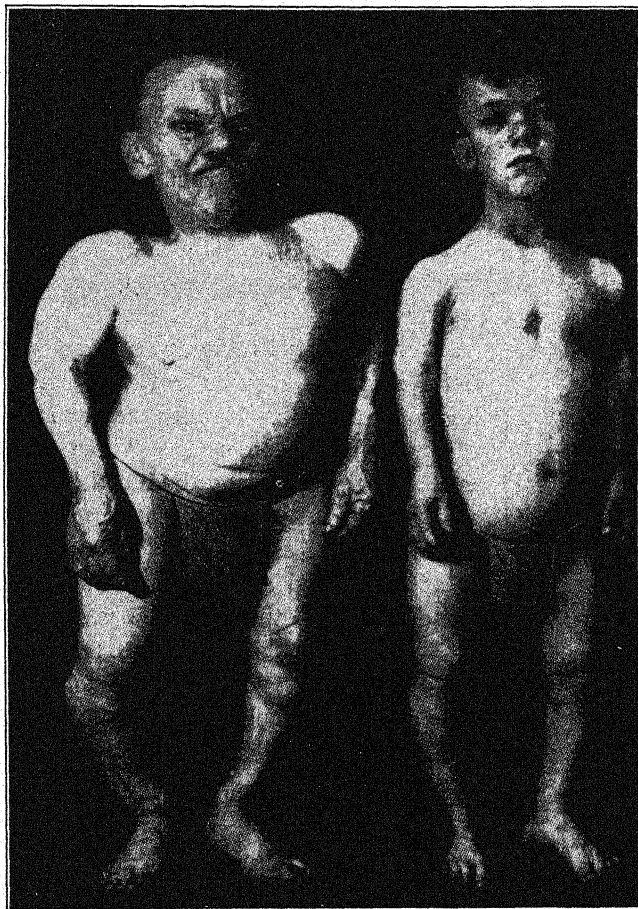


FIG. 124. Father and son showing inheritance of achondroplasia, a type of dwarfism characterized by a body of normal size and limbs very much shortened (*cf.* Fig. 125). This deformity is conditioned by a dominant gene which has arisen by mutation in a considerable number of different individuals.

(From E. T. Mörch, 1940, *Jour. Heredity*, vol. 31, reprinted by permission.)

who carry two recessive genes in their cells are albinos; their eyes appear pink because the blood vessels of the iris are not screened by pigment. Where pigment is deposited, another

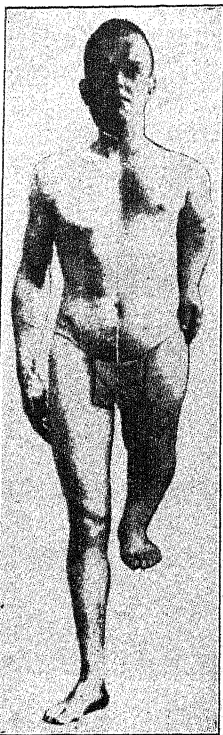


Fig. 125. Composite photograph showing localized shortening of limbs in the achondroplastic dwarf (*right side*) as compared with proportions of trunk and limbs in normal man (*left side*).

(From E. T. Mörch, 1940, *Jour. Heredity*, vol. 31, reprinted by permission.)

pair of genes conditions its distribution. Homozygous or heterozygous dominant individuals have a purple-black pigment behind the iris and brown pigment in front of the iris and appear brown-eyed. Homozygous recessive individuals have pigment only behind the iris and appear blue-eyed. The albino genes affect pigmentation of the skin and hair, as well as of the eye. Curly hair is dominant to straight hair. In color-blindness, which is the result of an inherited defect of the retina, and in hemophilia, a defect of the blood that prevents its clotting, the genes are sex-linked (Fig. 126). The production of the A, B, and Rh substances found in human red blood cells is determined by heredity (*cf.* pp. 100 and 155). The *Rh* gene is dominant, and individuals homozygous or heterozygous for it contain the Rh substance. In the A and B substances we have an example of multiple allelomorphs. Three allelic genes are known to condition the blood types, but only two of these genes occur in any individual. They are symbolized as *A* (gives A antigen), a^B (gives B antigen), and *a* (gives neither antigen). Individuals may, therefore, be genotypically *AA* or *Aa* and have blood of type A; $a^B a^B$ or $a^B a$ and have blood of type B; Aa^B and have blood of type AB; or *aa* and have blood of type O.

Mental as well as physical characteristics appear to be inherited. The evidence seems to indicate that mental qualities leading to degeneracy, crime, and pauperism, as well as those yielding leadership in all social fields, may be inherited according to Mendelian principles. It is not to be understood that there are special

genes determining crime or pauperism but rather that genes giving rise to defective mental equipment predispose to these undesirable social traits. In the same way the so-called inheritance of diseases

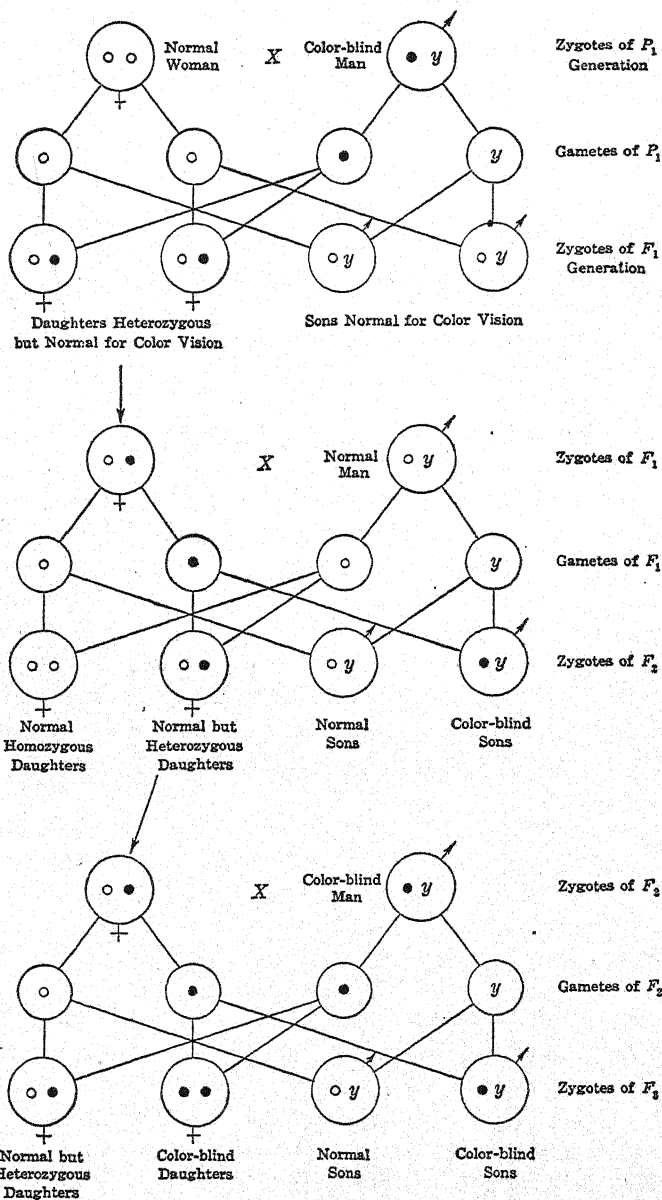


FIG. 128. Inheritance of color-blindness in man. The gene for a defective retina is located in the X-chromosome, which explains the crisscross transmission from a color-blind man to half the sons of his daughters. Color-blind daughters may occur if a woman heterozygous for color vision marries a color-blind man, as shown in the third cross. ♀ is the symbol for a female; ♂, the symbol for a male. ○ indicates an X-chromosome carrying a gene for normal color vision; ● an X-chromosome carrying a gene for color-blindness; y is the Y-chromosome of the male.

is an inheritance of morphological or physiological characteristics that render an individual more susceptible to infections. Instances of prenatal infection (*cf.* p. 154) are not cases of inheritance as the term has been used in this chapter.

The environment in which a particular gene-complex develops may limit and obscure its possibilities. Thus, a given combination of genes in a human individual may produce a better adult in a favorable environment than it could in an unfavorable one. On the other hand, a good combination of genes will give rise to a better individual in a particular environment than will a poor set of genes. Training is another element that is very important in the unfolding of human potentialities. An inferior inheritance with superior training may result in an individual better fitted for society than one with a good inheritance with no training. But no amount of training can produce anything for which the inherited capacities are not present, nor can the best of environments implant qualities the potentialities of which are lacking in the germ plasm. In other words, heredity limits very definitely the possibilities of training and environment.

Eugenics is that particular branch of applied genetics which deals with the improvement of the mental and physical characteristics of future generations of the human race. Its problems are: first, extension of our knowledge concerning human heredity; and, second, the education of the public in an appreciation of the meaning and application of this knowledge. The first of these problems is very difficult. A knowledge of hereditary principles is best gained from controlled and repeated experiments, which obviously cannot be carried out with human beings. Thus, the social tabu against marriages between near relatives is based on the knowledge that defective offspring result if recessive genes for undesirable traits are brought together. This, of course, can also occur in marriages between unrelated individuals. Inbreeding experiments with rats conducted by Helen Dean King for many years produced an unusually vigorous stock of animals. Animals having desirable genes in a homozygous condition will be obtained by inbreeding if the desirable genes are present in the beginning; neither defective nor desirable genes are produced by inbreeding. In 1930 H. S. Jennings in "The biological basis of human nature," pointed out the great handicaps of eugenics in the light of modern knowledge of genetics. The phenomenon of dominance makes heterozygous individuals appear normal, although they may transmit undesirable genes. Prevention of the breeding of the socially unfit, desirable as such a measure is, will not eliminate the heterozygous carriers. More needs to be known about the detection of carriers, and each

individual must be educated concerning his responsibilities to society in the production of offspring.

Heritable Variations

The genetic data so far presented indicate two general reasons why offspring are not exactly like their parents. In the first place, the environment may influence the developing young and produce a fluctuation, or somatic variation. As was pointed out in connection with Johannsen's studies on beans (p. 164), such variations are not inherited; they do not affect the germ cells. In the second place, the results of hybridization experiments show that new combinations of genes give rise to individuals differing from their parents. Disjunction and independent assortment of the pairs of chromosomes containing the linked genes of the several groups give rise to gametes different in their genic content. The random combination of gametes to form zygotes can produce a great number of phenotypes and more genotypes in cases where dominance occurs. The possibilities of new combinations of linkage groups are limited, however, by chance, and the same variations are produced many times. This sort of thing is sometimes said to be like dealing hands of cards. Many combinations can be dealt, but the cards themselves, which would be comparable to the chromosomes carrying groups of genes, remain unchanged and occur in the same numbers and kinds.

New combinations of genes may also arise as a result of changes brought about in any linkage group by the process of *crossing-over*. Crossing-over happens when comparable regions of homologous chromosomes become exchanged (Fig. 127) and gives rise to unexpected classes of offspring. If a male *Drosophila* with white eyes and a yellow body is mated to a female with red eyes and a gray body, all the F_1 offspring, both males and females, will have red eyes and gray bodies. The genes for these characters are known to be located on the X-chromosome, so that the ordinary expectation of F_2 can be easily ascertained by referring to Figure 119. If one of these heterozygous females with red eyes and gray bodies is then mated to a male with white eyes and a yellow body, 99 per cent of the offspring are of the expected kinds: equal numbers of males and females with red eyes and gray bodies and with white eyes and yellow bodies (Fig. 128). The other 1 per cent is made up of equal numbers of males and females with red eyes and yellow bodies and with white eyes and gray bodies. These individuals arise from zygotes containing chromosomes in which crossing-over has occurred. Crossing-over has been extensively stud-

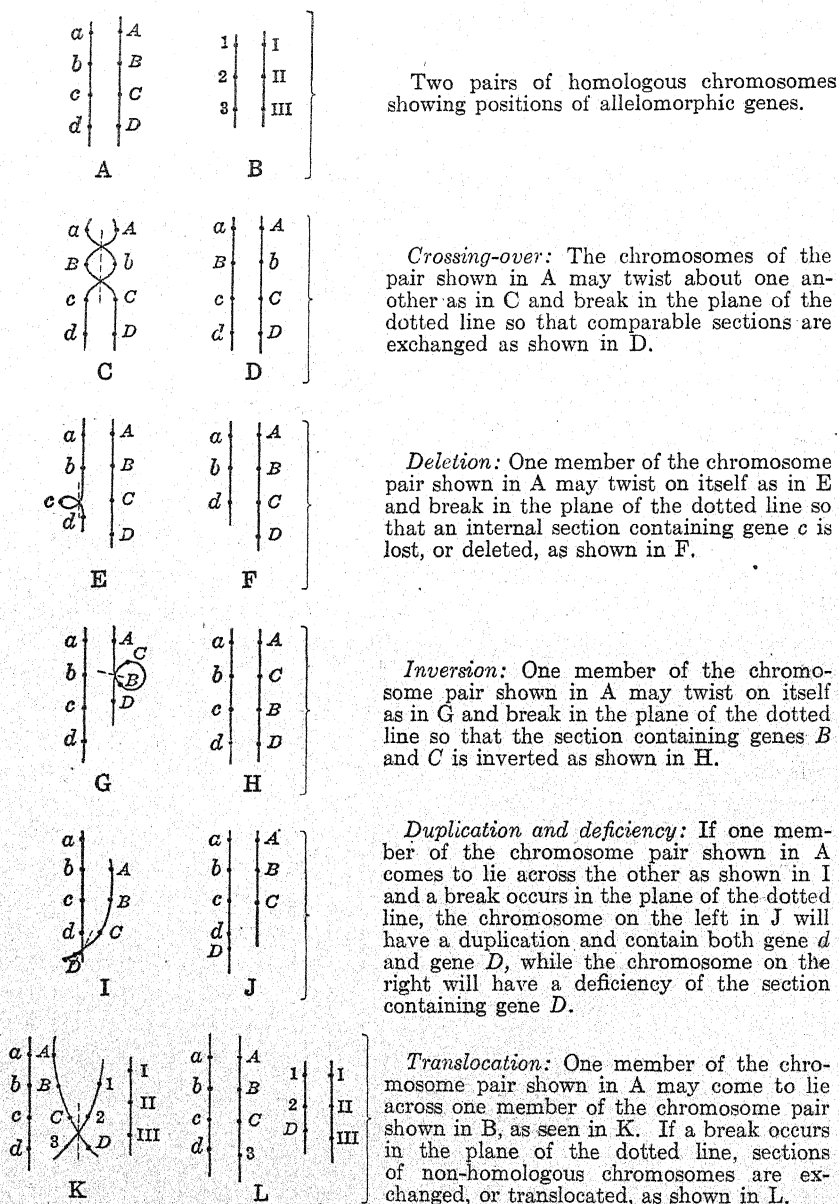


FIG. 127. Crossing-over and various chromosomal aberrations; diagrammatic.

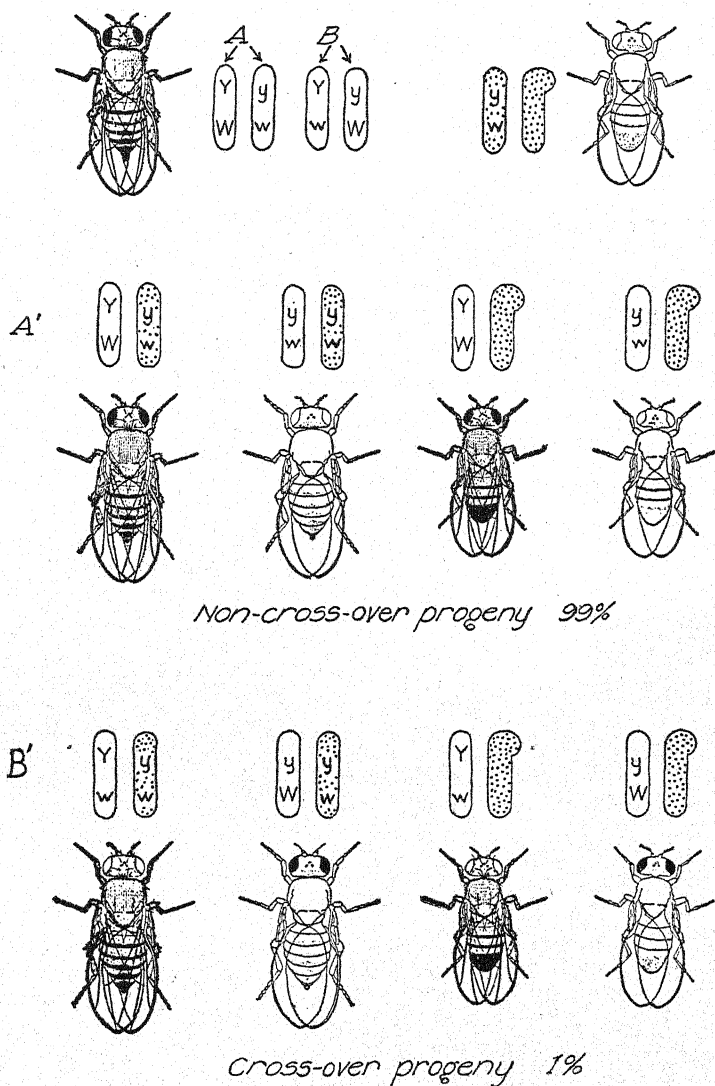


FIG. 128. The effect of crossing-over in a case of sex-linked inheritance. A heterozygous female *Drosophila* with red eyes and gray body is mated with a male which has white eyes and yellow body like her father. Ninety-nine per cent of the offspring (shown at A') are of the expected or non-cross-over types that result when the X-chromosomes at A pass into ova and combine with sperm. One per cent of the offspring (shown at B') have unexpected combinations of eye and body colors; these develop from zygotes that have received chromosomes in which crossing-over has occurred (shown at B). Chromosomes from the female are represented as empty, while those from the male are dotted. Y and y are the genes for gray and yellow body-color W and w for red and white eye-color (cf. Fig. 127 C and D).

ied, and the percentage of cross-over types to be expected in given crosses is known; the amount of crossing-over differs among different genes. The concept that genes are arranged in a given linear order was deduced from crossing-over, and chromosome maps showing the distances between the loci occupied by certain genes have been compiled from the data collected on crossing-over (Fig. 118).

The changes in combinations of entire linkage groups that occur from generation to generation as a result of disjunction of homologous chromosomes and subsequent combinations of gametes, as well as the changes in gene associations within linkage groups that arise from crossing-over, are merely shifting of genes without change of their quality or quantity; that is, the genes are present in the expected numbers and unaltered in kind. When the complete results of breeding are examined, however, we find that there are changes in single genes and in groups of genes which produce noticeable changes in the characteristics of an individual and which are heritable. Such heritable variations fall into two classes: those arising by an alteration, or mutation, of a particular gene, and those resulting from what are known as chromosomal aberrations which give rise to changes in the numbers of genes or in their relationships to one another in the linkage groups.

Gene mutations are ordinarily thought of as changes in the quality of a given part of the gene-string. Over 400 such mutations have been discovered in the thousands of *Drosophila* that have been examined, although the number of times that any particular mutation has occurred is very small (Fig. 129). One gene has been recorded as mutating 4 times in the formation of 500 gametes, another 2 times in 1800 gametes. When all the genes in chromosome II of *Drosophila* were considered it was found that only 30 mutations occurred in 5000 chances. Not all genes mutate with the same frequency, and very few, apparently, change often under normal conditions. Mutations produce changes in the structure of organisms and in the way they function. Many mutations that tend to alter function result in the death of the organism; they are called lethal mutations.

Chromosomal aberrations involve parts of chromosomes, whole chromosomes, and even entire haploid sets of chromosomes. The fact that losses or additions of genes in the cell produce observable changes in the individual reminds us that genes ordinarily interact with one another in what must be thought of as a balanced condition. If this balance is shifted by adding or subtracting groups of genes, the effect may be to kill the individual; in other cases, the individual may live

but be unable to produce functional germ cells. Sometimes such aberrations can be handed on from one generation to the next. The various types of alterations in linkage groups can be described briefly.

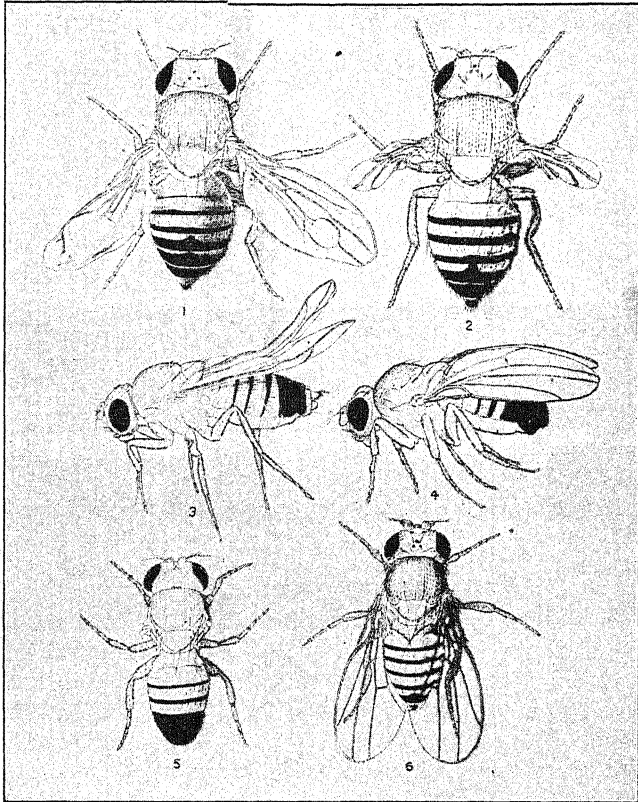


FIG. 129. *Drosophila* mutants, arising by gene mutations in chromosome II. The mutations are named as follows: 1, balloon wing; 2, vestigial wing; 3, jaunty wing; 4, arc wing; 5, apterous, or wingless; and 6, telescope abdomen.

(From C. B. Bridges and T. H. Morgan, 1919, Carnegie Institution Pub. 278.)

Alteration in a linkage group may be brought about by loss of a certain region of a chromosome. This is known as *deletion*, and an individual in which a deletion occurs will contain only one of each of the genes located in that region of the chromosome (Figs. 122 and 127). Sometimes breeding results indicate that *inversion* has taken place; that is, a portion of the gene-string has been reversed in position (Fig. 127). It is of considerable interest that alteration of the linear order may produce a heritable effect different from that resulting from

the same genes in their typical sequence. Occasionally, a part of one chromosome becomes attached to the other member of a pair in such a way that one chromosome has a given region *duplicated*, whereas its homologue is *deficient* for the same region and the genes it carries (Fig. 127). Another type of shift in linkage relations occurs when pieces of non-homologous chromosomes become interchanged (Fig. 127). This is known as *translocation*. What cytological evidence there is

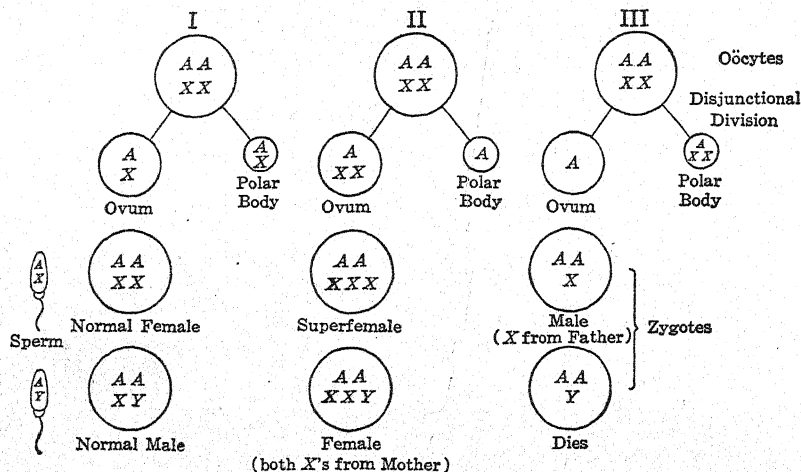


FIG. 130. Diagram showing, in column I, normal disjunction of the X-chromosomes in oögenesis and the subsequent possibilities of fertilization with typical sperm; in column II, non-disjunction of X-chromosomes, both remaining in the ovum, and subsequent fertilization; and in column III, nondisjunction of X-chromosomes, both passing to the polar body, and subsequent fertilization.

A is used as a symbol for a complete haploid set of autosomes.

concerning the chromosomal behavior responsible for these altered linkage relationships indicates that, when the chromosomes are in the form of long threads during the early growth period (cf. Fig. 64, p. 116), they may come into contact with one another, stick together, and sometimes be broken when the contractions of the threads occur.

An entirely different type of abnormal chromosomal behavior sometimes occurs during the meiotic divisions. Homologous chromosomes may fail to separate from one another and, therefore, will pass together into one cell. This is known as *non-disjunction* and can involve any pair of chromosomes. One resulting cell will lack a whole chromosome of the typical haploid set, whereas the other will have a haploid set plus one chromosome. Fertilization will result in some individuals which have only one chromosome of a particular pair, and

others which have three such chromosomes. These individuals will lack one complete gene-string or have an extra one. In *Drosophila* non-disjunction of X-chromosomes and of the smallest chromosomes (IV) is known to occur (Fig. 130). Non-disjunction of the X-chromosome gives rise to females and males with unexpected characteristics, since some females get both X-chromosomes from their mother and some males get an X-chromosome from their father. Non-disjunction of chromosome pair IV produces haplo-IV and triplo-IV individuals differing from one another and from the normal diplo-IV fly in appearance (Fig. 131). Entire sets of chromosomes may fail to disjoin, so that a gamete will contain the diploid rather than the usual haploid number of chromosomes. If fertilization adds a haploid set to such a diploid gamete, the zygote has three chromosomes of each kind and gives rise to a *triploid* individual. In *Drosophila* such flies are conspicuously different from the diploid or normal type (Fig. 131).

Individuals that have four or more chromosomes of each set are also known. They may arise as a result of an incomplete mitosis at the time of the first cleavage of the zygote. The chromosomes undergo reduplication but do not separate, so that the number is doubled and a *tetraploid* individual develops. Such organisms usually are conspicuously larger than their diploid relatives. Chromosome doubling sometimes occurs when gametes from two different species of plants have united. Subsequent synapsis between pairs of homologous chromosomes is thus made possible, and functional gametes may be formed. This usually does not occur in species hybrids, such as the mule. Several entirely new species of plants are known to have been established by chromosome doubling in a hybrid, but so far no comparable cases have been discovered among animals.

Since gene mutations and chromosomal aberrations offer very interesting material for the study of the mechanism of heredity, many investigators have attempted to increase the rate at which such alterations occur. *Drosophila* was subjected to high and low temperatures, various nutritional modifications, and treatment with a great many chemicals, but with no appreciable change in the frequency of the appearance of mutations. It remained for H. J. Muller to show in 1925-1926 that X-rays greatly increased the number of chromosomal aberrations, as well as gene mutations. In 1929 F. B. Hanson and Florence Heys demonstrated that radiations from radium were also effective, and that mutations were induced three times more frequently in flies reared in an abandoned mine, where some radioactive material was still present, than in those reared in the laboratory.

Heritable variations are the only source of new kinds of organisms, the material of organic evolution (*cf.* pp. 705-714). Man has made use of natural mutations in establishing new races of domestic animals.

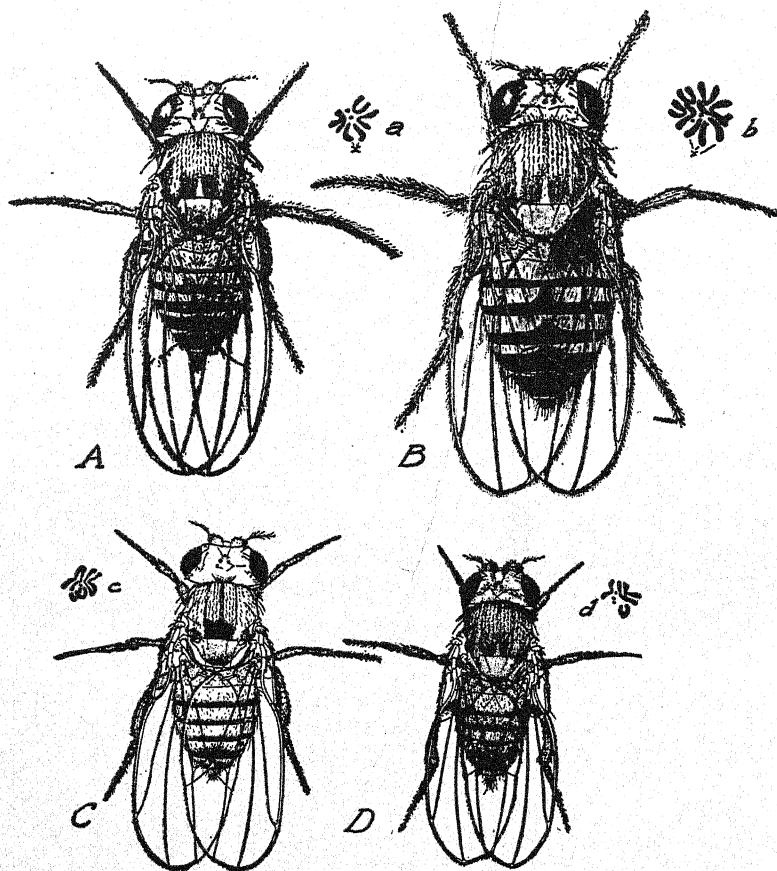


FIG. 131. A normal female *Drosophila* at A is shown for comparison with a triploid female at B, and with haplo-IV and triplo-IV females at C and D, respectively. The chromosomal constitution for each of these flies is shown in the groups at a, b, c, and d.

(From T. H. Morgan, C. B. Bridges, and A. H. Sturtevant, 1925, *Bibliographia genetica*, vol. 2.)

such as short-legged Ancon sheep and polled Hereford cattle. New varieties of plants have likewise been obtained. It is entirely possible that the use of radiation may produce some mutations of great economic value to man, along with the many that increase our store of knowledge about genetics. In no field of biological science is re-

search more active than in genetics. This section has touched upon some of the recent advances and the problems that confront the geneticist of today.

Sex Determination

Animals are typically *diœcious*; that is, there are two sexes, which differ essentially in that the males produce microgametes, or spermatozoa, whereas the females produce macrogametes, or ova. In association with this primary distinction between males and females, we have seen that differences exist between the reproductive systems (cf. p. 121). In many cases what are known as secondary sex characters are very conspicuous distinguishing features of the sexes. For example, the gay plumage of many male birds, the vocal differences between the sexes in many vertebrates from frog to man, and in some mammals the greater growth of hair in the males, as in the lion and man, differentiate the sexes. It is true that in numerous species of vertebrates, especially among lower animals, no such secondary sex characters can be observed, although there may be a size difference between the sexes.

Not all animals are sexually distinct; some are *monœcious*, or *hermaphroditic*, and every individual produces both microgametes and macrogametes. Sometimes hermaphroditic animals produce first sperm and later eggs, or *vice versa*, but frequently eggs and sperm are matured at the same time. Almost all plants are monœcious. We see, therefore, that sexuality among individuals is not by any means a universal attribute of living things. The production of differentiated gametes correlated with the capacity of reproduction is not dependent upon the sexual differentiation of individuals.

The conspicuous differences between the sexes in the higher animals have long excited the curiosity of biologists and led to attempted explanations and hopes for control. Early hypotheses were formulated in terms of the nutritive conditions under which the young developed, in spite of the obvious fact that a litter of pups or kittens, for example, contains both males and females whose development has occurred under identical conditions. In man two kinds of twins are known. Fraternal twins may be of the same or opposite sex and bear no more resemblance to one another than other brothers and sisters, but identical twins are always of the same sex. A comparable situation is known in the nine-banded armadillo, which gives birth to four young, all of the same sex, and in certain insects, which produce by the method of polyembryony large numbers of young all of the same sex. These situations were clarified by study which revealed that identical

twins in man and other mammals and the quadruplets of the armadillo, as well as the polyembryos of insects developed from single zygotes, had identical hereditary constitutions.

Furthermore, the discovery and study of the so-called sex chromosomes led to the interpretation proposed by E. B. Wilson in 1905 that sex was determined at the time of fertilization by the chance combinations of the gametes formed. In the insect, *Protenor*, there are 14 chromosomes in the female but only 13 in the male (cf. Fig. 60, p. 111); 7 pairs of chromosomes in the female, but only 6 pairs and an extra or odd chromosome in the male. The extra chromosome of the male can be clearly seen to be similar to one of the pairs of the female, the largest pair in this instance. This unpaired chromosome of the male and the comparable pair of the female are called X-chromosomes or *sex chromosomes*. All the other chromosomes, which occur in pairs in both males and females, are known as *autosomes*. If a haploid set of autosomes is designated as A , then a formula for the chromosome number of any somatic cell or primordial germ cell of a female *Protenor* would be $2A + 2X$, where X stands for a sex chromosome, and the formula for every mature ovum would be $A + X$. The chromosome content of somatic cells and undifferentiated germ cells of a male *Protenor* would be $2A + X$. One half of the spermatozoa could be represented by $A + X$, and the other half by $A + 0$. Wilson pointed out that, when an ovum ($A + X$) was fertilized by one kind of spermatozoön ($A + X$), the zygote would have the number of chromosomes characteristic of the female ($2A + 2X$). If the ovum ($A + X$) was fertilized by the other kind of spermatozoön ($A + 0$), then the zygote would have the number of chromosomes characteristic of the male ($2A + X$). Since by the process of mitosis during development each cell receives the same number of chromosomes that the zygote has, it can be seen how the concept arose that sex was determined by the number of X-chromosomes present in the zygote.

It was soon discovered that the male did not always differ from the female in number of chromosomes and that, although the male had only one X-chromosome, it sometimes had a Y-chromosome that segregated from the X-chromosome at the disjunctive division (cf. Fig. 63, p. 115). The Y-chromosome, like the X, is known as a sex chromosome. *Drosophila* males have such a Y-chromosome (cf. Fig. 60, p. 111) and produce two classes of spermatozoa, which can be represented as $A + X$ and $A + Y$. Union with $A + X$ ova yields female-producing zygotes ($2A + 2X$) and male-producing zygotes ($2A + XY$). In *Protenor*, which is an example of forms with X0 males, and *Drosophila*, which is an example of forms with XY males, the males are the

digametic sex, or the sex that gives rise to two kinds of gametes with respect to the X-chromosome.

The diagrammatic simplicity of such a method of sex determination became somewhat confused when the observation was made that in some species of moths and in birds the female was the digametic sex; that is, a female moth produces two kinds of ova, one with an X-chromosome and one without, whereas all the spermatozoa are alike in carrying an X-chromosome. However, many facts indicate an undeniably close correlation between number of X-chromosomes and

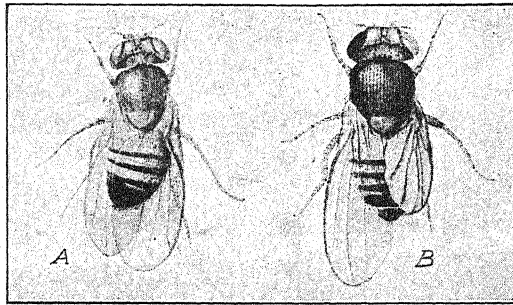


FIG. 132. Bilateral gynanders of *Drosophila*. The right side of the individual at A is female, and the left side is male; since the male has a shorter body, many gynanders of this type have curved abdomens. The specimen at B is an eosin-eyed male with miniature wings on its right side, and a red-eyed female with long wings on its left side.

(From T. H. Morgan and C. B. Bridges, 1919, Carnegie Institution Pub. 278.)

sex. One of the most interesting is the occurrence of bilateral *gynanders*, which are male on one side and female on the other (Fig. 132). It is clearly established that gynanders in *Drosophila*, for example, arise from female-producing zygotes ($2A + 2X$). At the time of the first division one of the X-chromosomes, either the paternal or the maternal, is lost on the mitotic spindle, so that one nucleus has $2A + 2X$ chromosomes and the other has $2A + X$ chromosomes. The former gives rise to the female half, the latter to the male half of the gynander. If the X-chromosome is lost in some later division, only a limited region of the female will exhibit male characteristics.

In spite of such confirmation of the sex-chromosome theory of sex determination, it should be obvious that the study of inheritance has shown that characters depend on combinations of the genes located in the chromosomes, not on the chromosomes as such. Yet with sex, the presence of two particular chromosomes was assumed to condition the differentiation of one sex, while one of these chromosomes was as-

sumed to condition the differentiation of the other sex. Either one of the X-chromosomes of a female could enter a male-producing zygote, and the X-chromosome of a male could pass into a female-producing zygote. No gene for maleness or femaleness has been located on the chromosome maps of *Drosophila* nor with certainty been identified in any species, although reported by some investigators (Fig. 118). The discovery of intersexes among the offspring of triploid females (Fig. 131) by C. B. Bridges in 1921 led to his formulation of the *Theory of Genic Balance* to explain the determination of sex. When disjunction occurs in the germ cells of triploid ($3A + 3X$) females, some eggs with $2A + X$ chromosomes and some with $A + 2X$ are formed, among others. If a $2A + X$ ovum is fertilized by an $A + X$ sperm, a $3A + 2X$ zygote results and develops into an *intersex*, or an individual that is male in some parts and female in others (Fig. 133). These male and female parts are not clearly segregated into halves or quarters as in gynanders but are completely blended, and intersexes range from almost total females to almost total males. Bridges' theory is that sex is the result of the interaction of many different genes, some of which are to be thought of as female determiners and others as male determiners. Both types of genes are located on all the chromosomes. However, there are more female than male determiners in the X-chromosomes, whereas the reverse situation is true in the autosomes. The distribution and effect of these genes are such that, when a zygote has a $2A + 2X$ constitution, the female determiners on the X-chromosomes overbalance the male determiners on the autosomes. When the zygote has a $2A + X0$ or $2A + XY$ constitution, the male determiners on the autosomes overbalance the female determiners on a single X-chromosome; the Y-chromosome appears to carry no genes related to sex. In the $3A + 2X$ individuals neither set of genes overbalances the other, but both are somewhat effective in molding the appearance of the intersex. This theory is strengthened by the occurrence of what are known as superfemales and supermales in which the chromosomal make-up is $2A + 3X$ [ovum ($A + 2X$) + spermatozoön ($A + X$)] and $3A + XY$ [ovum ($2A + X$) + spermatozoön ($A + Y$)], respectively (Fig. 133). Although triploid ($3A + 3X$) and tetraploid ($4A + 4X$) individuals are females, as would be expected on the basis of an explanation in terms of genic balance, haploid individuals ($A + X$) are males in bees and other forms that normally produce males parthenogenetically. Haploid drosophilas have not been found, so that the theory remains untested in a crucial case. More facts are necessary before the final word can be said on the mechanism of sex determination at fertilization. We have seen an apparently satisfactory theory

in terms of $2X$ versus $X0$ or XY zygotes fail to explain accumulated observed facts and hence undergo modification. Such is the method of science: observation, explanation, further observation or experimentation, and modification of explanation when necessary—a continued seeking for the whole truth.

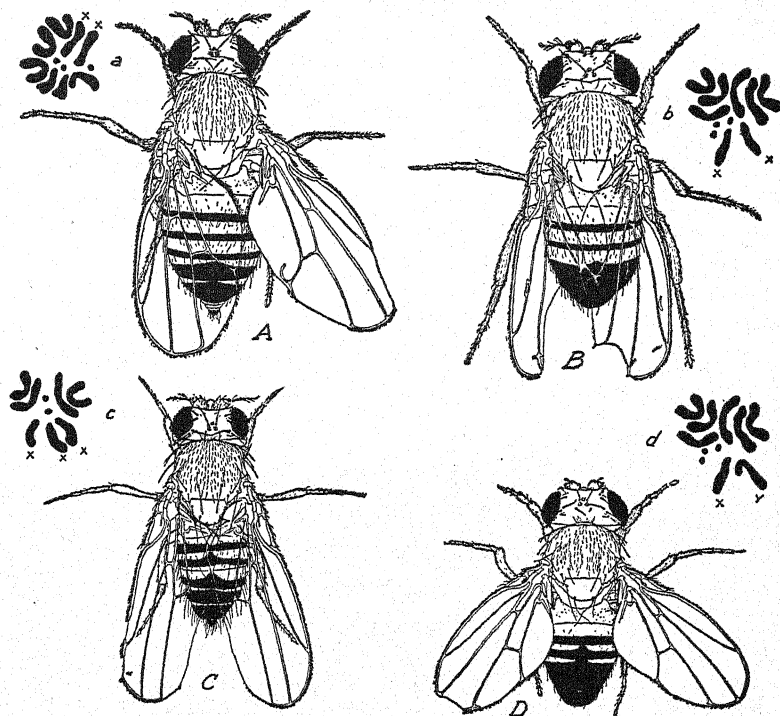


FIG. 133. Intersexes and supersexes in *Drosophila*; these occur in the progeny of triploid females. A, female-type intersex. B, male-type intersex. C, superfemale. D, supermale. Chromosome groups for A, B, C, and D are shown at a, b, c, and d, respectively.

(Adapted from T. H. Morgan, C. B. Bridges, and A. H. Sturtevant, 1925, *Bibliographia genetica*, vol. 2.)

As in all development, the environment influences the differentiation of so-called sex characters. A zygote in which the genic balance is female-determining may develop into a male in an atypical environment. In 1915 Emil Witschi found that, if frogs were forced to develop at a high temperature, they were all males because the female-producing genotype had been overridden by environmental conditions. Sometimes reversal of sex occurs. A hen, for example, may change into a cock and produce spermatozoa. Although the mechanism of the

overriding of the inherited constitution, the genotype, is not clear, this is only a special case of the effect of the environment, as noted previously (cf. pp. 158 and 188).

The problem of sex determination is not really a special one, although it has long been so treated. It is well known by geneticists that single pairs of genes do not by themselves produce an effect in the organism. They always depend upon the presence of other genes, upon a given pattern of distribution of the cytoplasm of the zygote during cleavage and the cell movements during development, upon interactions between differentiating cells, and upon the chemical and physical conditions of the external environment. In the ordinary course of events the genes are the part of this complex most often varied; that is, new combinations of genes occur with each fertilization, but development proceeds under practically uniform conditions in the great majority of cases. When the environment is altered, its importance in the complex of factors determining what the individual will be, not only with respect to its sex but also its other characteristics, is appreciated.

Dear Sam Hosh.
Malhotra.

CHAPTER 7

CLASSIFICATION AND ORGANIZATION OF ANIMALS

In the preceding chapters an introduction to zoölogy has been secured through an intensive study of structure and function in the animal type that is most familiar. The organization of vertebrate animals and the capacities of metabolism, irritability, and reproduction have thus been illustrated, and, in addition, the nature of development and heredity has been indicated. On the functional side this study would suffice for animals in general, because the capacities of protoplasm are similar in all animal bodies. On the structural side it is inadequate, because there are kinds of animals very different from vertebrates in their organization, however similar their functions. In the series of chapters that follow, these different kinds of animals will be examined in illustration of principles in the fields of morphology, ecology, and evolution. Classification of the Animal Kingdom as a whole and related problems are appropriate introductions to such a survey.

Classification

Historical. The first attempt to classify animals scientifically was made by Aristotle (384-322 B.C.). Later, various groupings were made and comparisons were even drawn between the structures of plants and those of animals, although the classification that developed into the present system was not formulated until the eighteenth century. In general the classification of plants progressed more rapidly than that of animals. Thus, Ray (1628-1705) attempted to classify both plants and animals in a similar manner and emphasized structure as the basis of classification. He limited the term species to forms that produce offspring like themselves when bred together, a definition in accordance with the subsequent use of this important term. However, it remained for Linnæus (1707-1778), who is justly called the Father of Classification, to establish the classification of plants and animals (1758) that was the beginning of present-day systems, although little now remains of the details or the generalities he laid down. In his youth Linnæus became interested in botany, and he was always more a botanist than a zoölogist, although his zeal led him to study animals and to formu-

late a classification that included all known animals as well as plants. As might have been expected, his work with animals was not so successful as that with plants. Nevertheless, his use of structure as the basis for classification; his establishment of the *binomial nomenclature*, by which organisms are given generic and specific names; and the working out of the Linnaean system in general, which became widely accepted and was the beginning of our modern system, justify his enduring fame in this field of biological science.

The Modern System. It is a familiar fact that animals fall into restricted groups called species (singular, "species," not "specie"), which may be defined as groups whose members will interbreed and are more like one another than like any members of other similar groups. The individuals, which are the ultimate material of classification, can thus be grouped into species, species into larger groups, and so on. This may be illustrated by beginning with the individuals and species, as did investigators in the first instance, or, as the system is now established, by beginning with one of the major groups and following its subdivisions until the species and individuals are reached. For example, the existence of a large group of animals known as *Vertebrata* was recognized after it had been discovered that a great array of animals possessed backbones composed of vertebræ. Later it was found that several types of animals without vertebræ and with a relatively simple organization possessed certain features in common with vertebrates, particularly a notochord such as occurs in the early vertebrate embryo. The *Vertebrata* were then placed, along with these simpler forms, within a larger group, constituting a *Phylum*, or one of the principal subdivisions of the Animal Kingdom. This *Phylum Chordata* includes a wide range of animal types despite the fact that all chordates have features in common (Figs. 147-149). Distinguishing characteristics are the presence, in the adult or at some stage of development, of a primitive skeletal axis, the notochord, from which the name chordate is derived; gill slits or rudiments of these parts; and a dorsal, tubular, central nervous system.

The principal subdivisions of the *Phylum Chordata* are listed in the table appearing as Figure 134. One of these subdivisions is the Subphylum *Vertebrata*, including, along with others, the Class *Amphibia*, in which the forms now existing may be classified, as follows:

Class, *Amphibia*

Order, *Caudata*, salamanders, newts, etc. (Fig. 147 Below)

Order, *Apoda*, footless, wormlike forms (Fig. 448, p. 612)

Order, *Salientia*, frogs and toads (Fig. 449, p. 613)

After the *orders*, as one proceeds to smaller groups, come *families*, then *genera*, and finally *species*. Thus, the Order *Salientia* contains, along with some half-dozen others, the Family *Ranidæ*, which in turn includes the Genus *Rana* and other genera. For example:

Order, *Salientia*

Family, *Ranidæ*

Genus, *Rana*

Species, *Rana pipiens* Schreber, the leopard frog

In referring to a species, it is customary to use both the generic and the specific names, as one uses a family name and a given name in writing, "Smith, John," instead of merely "John" or "Smith." One refers to the species called the leopard frog as *Rana pipiens* Schreber, or *R. pipiens*, writing the generic name with a capital and the specific name with a small letter. In the complete form this is followed by the name of the individual who originally described the species, and the date of the description follows in parentheses. The following are common species of the Genus *Rana*: *R. catesbiana*, the bullfrog; *R. clamitans*, the green frog; *R. sylvatica*, the wood frog; *R. palustris*, the pickerel frog; and *R. pipiens*, the leopard frog.

A species containing groups of individuals with slight but constant structural differences is often divided into *varieties*. The amount of difference between the individuals composing any one species can be appreciated only by examining specimen after specimen and making comparisons. In general, the differences that separate varieties within species are less than those separating species. Whether a group shall be called a variety of an existing species, a new species, or even a new genus, depends upon the judgment of the individual making the classification. Some classifiers, the "splitters," tend to make many species; others, the "lumpers," make few species from the same collection of specimens.

The foregoing system of cataloging species illustrates the principles of classification that are followed at the present time. Beginning with a group of animals, such as a species of frog or grasshopper, one can follow it into larger and larger groupings until the Phylum is reached, and finally the *Animal Kingdom*, which is coördinate with the other great group of living things, the *Plant Kingdom*. Conversely, if one should begin with the Animal Kingdom, he might follow it into every subdivision until all the species were reached, and pass in review the diversified forms of animal life that are known. Present knowledge of classification is the result of study, in which hundreds of thousands of species have been described and arranged in the manner indicated.

I. SUBKINGDOM PROTOZOA

PHYLUM PROTOZOA

Subphylum Plasmodroma.

Class Sarcodina

Class Mastigophora

Class Sporozoa

Subphylum Ciliophora

Class Ciliata

Class Suctorina

I. SUBKINGDOM METAZOA

PHYLUM MESOZOA

PHYLUM PORIFERA

Class Calcarea

Class Hexactinellida

Class Demospongiae

PHYLUM CœLENTERATA

Class Hydrozoa

Class Scyphozoa

Class Anthozoa

PHYLUM CTENOPHORA

Class Tentaculata

Class Nuda

PHYLUM PLATYHELMINTHES

Class Turbellaria

Class Trematoda

Class Cestoda

PHYLUM NEMERTINEA

PHYLUM ASCHELMINTHES

Class Rotatoria

Class Gastrotricha

Class Echinoderida

Class Nematoda

Class Nematomorpha

PHYLUM ACANTHOCEPHALA

PHYLUM ENTOPROCTA

PHYLUM BRYOZOA

PHYLUM PHORONIDA

PHYLUM BRACHIOPODA

PHYLUM SIPUNCULOIDEA

PHYLUM PRIAPULOIDEA

PHYLUM ECHIUROIDEA

PHYLUM MOLLUSCA

Class Amphineura

Class Gastropoda

Class Scaphopoda

Class Pelecypoda

Class Cephalopoda

PHYLUM ANNELIDA

Class Archannelida

Class Polychæta

Class Oligochæta

Class Hirudinea

PHYLUM ARTHROPODA

Subphylum Branchiata

Class Crustacea

Subphylum Tracheata

Class Onychophora

Class Myriapoda

Class Insecta

Subphylum Arachnida

Class Arachnida

PHYLUM CHÆTOGNATHA

PHYLUM ECHINODERMATA

Subphylum Pelmatozoa

Class Cystoidea (Extinct)

Class Blastoidea (Extinct)

Class Crinoidea

Subphylum Asterozoa

Class Asteroidea

Class Ophiuroidea

Subphylum Echinozoa

Class Echinoidea

Class Holothuroidea

PHYLUM CHORDATA

DIVISION ACRANIATA

Subphylum Hemichordata

Subphylum Urochordata

or Tunicata

Subphylum Cephalochordata

DIVISION CRANIATA

Subphylum Vertebrata

SUPERCLASS Pisces

Class Agnatha

Class Placodermi (Extinct)

Class Chondrichthyes

Class Osteichthyes

SUPERCLASS Tetrapoda

Class Amphibia

Class Reptilia

Class Aves

Class Mammalia

FIG. 134. Phyla of the Animal Kingdom and their principal subdivisions.

This grouping is necessary as a means of cataloging the multitudinous organisms that compose the Animal Kingdom.

But classification, as now undertaken by zoölogists and botanists, is more than a cataloging system. The basis of classification is structure; and structure, the biologist believes, tells the story of ancestral relationships. Since the acceptance of evolution, which came after the publication of Darwin's "Origin of species" in 1859, classification has become a never-ending attempt to express evolutionary relationships as well as to furnish a catalog of living things. The functions of the parts of the animal or plant are not important for this purpose, because comparable parts often have entirely different functions in animals of the same phylum. The fundamental structure of the parts is important, because this structure is found to be the same despite the different uses of comparable structures in different animals. Consider, for example, the limbs of vertebrates. At the present time many species remain to be cataloged, and the "family tree" of life cannot be drawn with certainty in some of its general features, although many lesser features can be depicted with as much certainty as events in human history concerning which the data are incomplete. On this basis the tree of descent shown in Figure 150 is presented. Before we consider what this figure means, the catalog of animal life as now set forth should be examined.

The Principal Types of Animals. In accordance with the foregoing principles of classification, by which animals are arranged in species, genera, families, and so on, until the phyla and larger subdivisions are reached, zoölogists have arrived at the present comprehensive system (Fig. 134). Sweeping changes have been made in the past as additional knowledge has necessitated, for example, the separation of the Linnæan Phylum *Vermes*, or "worms," into several distinct phyla. Further changes will be made if necessitated by increasing knowledge, although it seems that classification into phyla and their main subdivisions now rests upon a fairly permanent foundation.

During the early years of the present century there was wide acceptance of a system including a dozen or fifteen phyla, to which lesser groups of questionable affinity were appended. Recently the tendency has been toward an increasing number of phyla in recognition of distinctive features in many of the lesser groups. There are twenty-three phyla distinguishable at the present time, according to Hyman, whose classification has been drawn upon to a considerable extent in the present edition of this textbook.¹

¹ Hyman maintains: "A phylum should consist of closely allied animals distinguishable from any other phylum by well-defined positive characteristics, some

Some of these phyla are small in the number of species, and others consist of animals not easily available and hence relatively unknown even to most zoölogists. For the purpose of the present chapter only the larger and well-known phyla need be considered in any detail. It can then be remembered that the Animal Kingdom includes certain lesser types, which may also be classified as phyla, and that authorities differ on many details of classification even today. For example, some make the Hemichordata a separate, though small, phylum; others place the Hemichordata in the Phylum Chordata (Fig. 134). The phyla that are thus important for our purposes are illustrated by Figures 136-149, which should be carefully studied with their explanatory legends. The list of phyla and their principal subdivisions presented in Figure 134 is inserted for reference. As the student proceeds, the names of the larger phyla, such as the Protozoa, Cœlenterata, Mollusca, and Chordata, as well as some of their subdivisions, will become familiar.

The phyla having been listed, the question arises whether they can be arranged in larger groups. To illustrate such an attempt to group the phyla, one may proceed as shown by Figure 135. Taking the Animal Kingdom as a whole, one may ask what is the greatest difference between the various kinds of animals. If all animals are to be divided into two groups, on what basis should they be separated? It may be answered that a separation can be made into the Subkingdom *Protozoa*, or the single-celled, and the Subkingdom *Metazoa*, or the many-celled animals. The Protozoa are thus placed apart from the remainder of the Animal Kingdom.

Proceeding, one may ask a similar question for the Metazoa. Can all many-celled animals be divided into two, or at least a few, principal groups? In the arrangement here given, the Metazoa are divided into three such groups: the Branch *Mesozoa*, which consists of a small number of species called the Phylum *Mesozoa*; the Branch *Parazoa*, which consists of the Phylum *Porifera*, or sponges; and the Branch *Eumetazoa*, which includes all other phyla. In turn, the Eumetazoa can be separated into two groups: the Grade *Radiata*, which consists of the radially symmetrical forms comprising the Phylum *Cœlenterata* of which do not exist in other phyla or not in that particular combination. Any group of animals, however small, having such distinct characters, should be regarded as a separate phylum until evidence shall be forthcoming showing its relationship to some other phylum." From L. H. Hyman, "The invertebrates: Protozoa through Ctenophora," McGraw-Hill Book Company, 1940, p. 32. In correspondence with the authors, November, 1945, Hyman adds the *Acanthocephala* as a phylum, making a total of twenty-three phyla instead of twenty-two, as listed in her textbook.

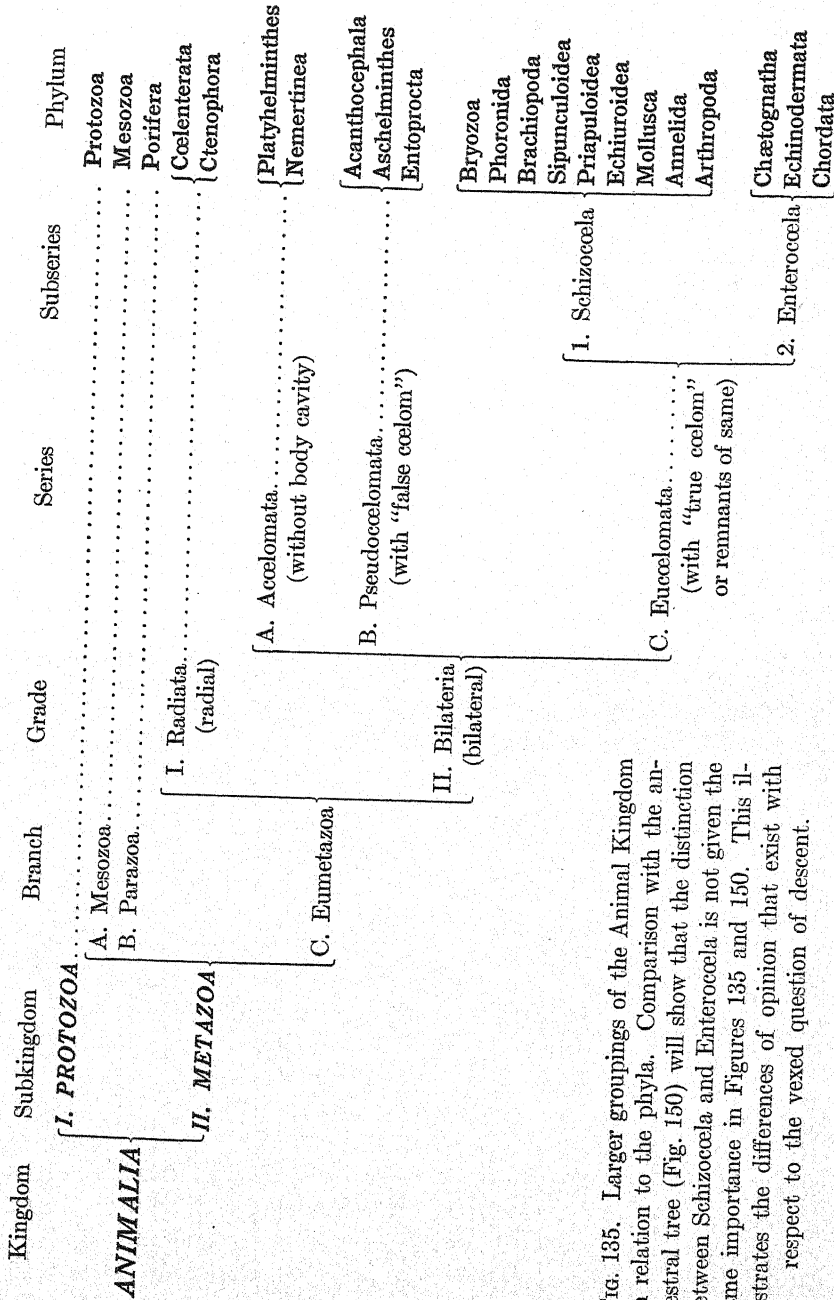


Fig. 135. Larger groupings of the Animal Kingdom in relation to the phyla. Comparison with the ancestral tree (Fig. 150) will show that the distinction between Schizocoela and Enterocoela is not given the same importance in Figures 135 and 150. This illustrates the differences of opinion that exist with respect to the vexed question of descent.

and the Phylum *Ctenophora*; and the Grade *Bilateria*, which includes all remaining phyla, the members of which are bilaterally symmetrical, although some of them, like the Phylum *Echinodermata*, have acquired a secondary radial symmetry.

Again, the Grade *Bilateria* can be divided into three principal subdivisions: the *Acœlomata*, which have no cœlom; the *Pseudocœlomata*, which have what can be called a "false cœlom"; and the *Eucœlomata*, which have a "true cœlom." The *Eucœlomata* can then be grouped as *Schizocœla* and *Enterocœla*, according to the origin of the cœlom: whether it has arisen as a cleft in the mesoderm cells of the embryo, a *schizocœl*, or as outgrowths from the embryonic gut, an *enterocœl*. It will be noted that the familiar segmented or metameric animals, such as the earthworms, insects, and vertebrates, are not classified all together in the same subdivision of the *Eucœlomata*. Also, this grouping of the phyla disregards the three *germ layers*, the *ectoderm*, *mesoderm*, and *endoderm*, which are used in some classifications for setting off the major subdivisions of the Animal Kingdom. Instead, the kind of symmetry, the presence or absence of a cœlom or body cavity, and the nature of this cavity are used to distinguish the *Radiata*, *Bilateria*, *Acœlomata*, *Pseudocœlomata*, and *Eucœlomata* and their subdivisions.

Since the presence or absence of a cœlom is thus used in classification, it is important to know what is meant by this term. The gut cavity or enteron is easily recognized and characteristic; it seems to be the same kind of a cavity and to be present in all the phyla, except the Protozoa, Mesozoa, and Porifera. The so-called body cavity, which lies between the body wall and the gut wall in various kinds of animals, does not seem to be the same kind of a cavity in all cases. Any such cavity that is fairly well defined can be called a body cavity, since this is a non-committal term. As used for making distinctions within the classification shown, the cœlom is a particular kind of body cavity. Some zoölogists think that any body cavity may as well be called a cœlom, so great is the confusion. Yet there seem to be different kinds of body cavities; and many zoölogists believe that the distinction can be drawn between a "false cœlom," or *pseudocœl*, and a "true cœlom," which has a characteristic relationship to the reproductive and excretory organs and which is lined by peritoneum (cf. Fig. 427, p. 570). This true cœlom may arise as a *schizocœl*, so called because it appears during development as clefts in the mass of mesoderm cells, or an *enterocœl*, which arises from pouches that grow out and separate from the gut cavity early in development. Hence, the terms *Acœlomata*, *Pseudocœlomata*, and *Eucœlomata* are used in the classification shown in Figure 135.

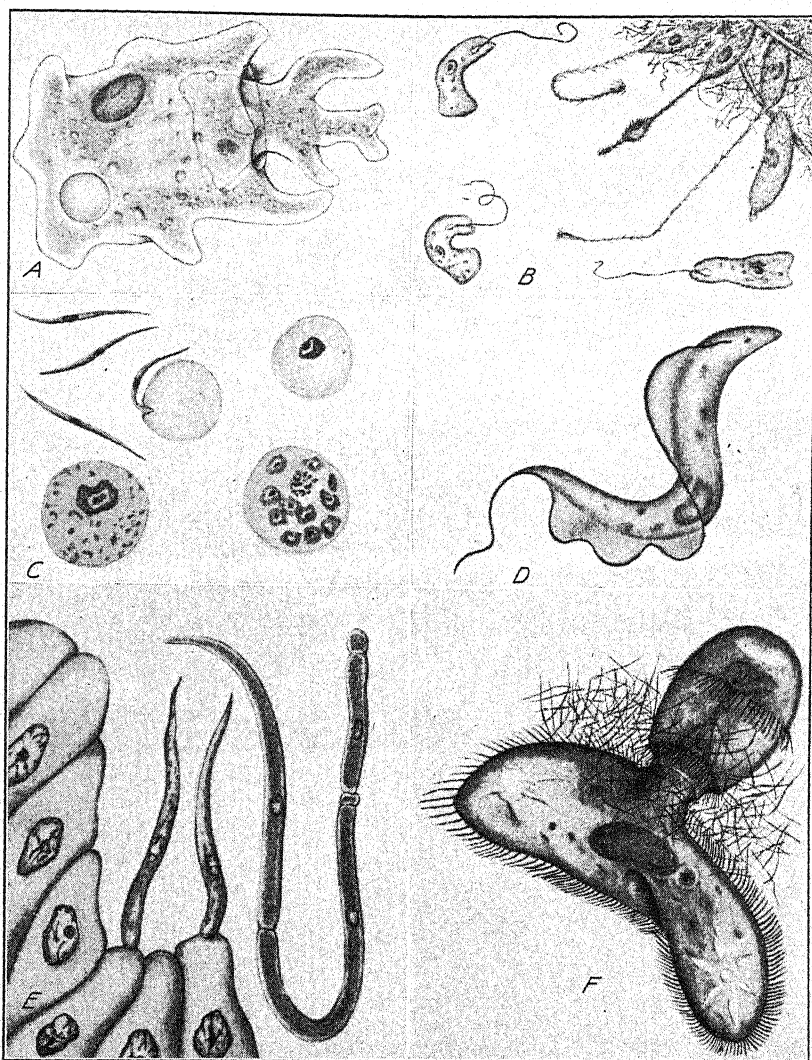


FIG. 136. Representative Protozoa. *A*, an amoeba in locomotion and capturing another amoeba. *B*, the flagellate, *Peranema*, assuming characteristic outlines; and the ciliate, *Lacrymaria*, which feeds by extending its anterior end, where cell mouth is located. *C*, the malaria parasite, *Plasmodium*, free in human blood, entering a blood cell, and reproducing by cell division. *D*, the parasite of African sleeping sickness, *Trypanosoma*. *E*, parasitic protozoan, *Porospora*, attached to cells in digestive tract of its host, a crab; and individuals attached end to end. *F*, the ciliate, *Didinium*, attacking another ciliate, *Paramecium*.

(Drawn to different scales, by Charles Schwartz under direction of W. C. Curtis.)

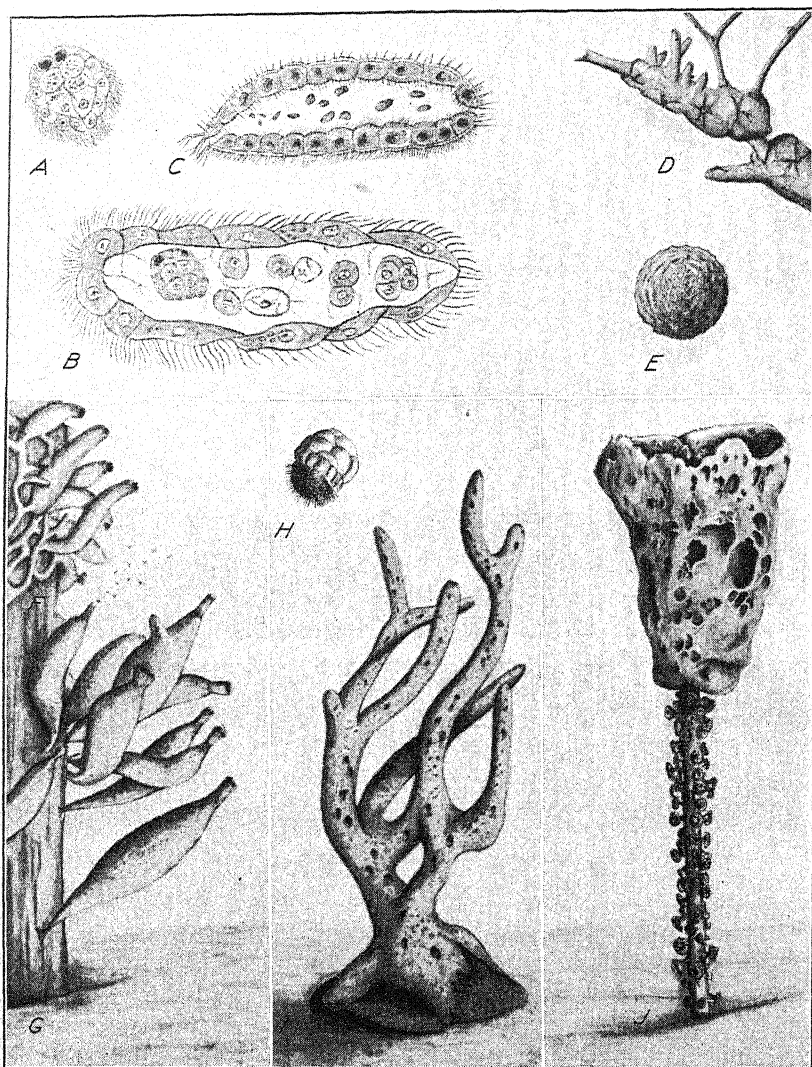


FIG. 137. Representatives of the simplest many-celled animals, Mesozoa and Porifera (cf. Figs. 135 and 150). *A* and *B*, the mesozoan, *Dicyema*, an asexual individual within which sexual individuals are developing, and one such individual of the male sex after liberation (after Hartmann). *C*, the mesozoan-like form, *Salinella* (after Frenzel). *D*, fresh-water sponge, *Spongilla*, growing upon submerged brushwood. *E*, gemmule of a fresh-water sponge, much enlarged (cf. Fig. 205, p. 308). *F* and *G*, the calcareous sponges, *Leucosolenia* and *Sycon*; larvæ are shown issuing from one of the individuals. *H*, free-swimming ciliated larva of *Sycon*. *I*, the "finger sponge," *Chalina*. *J*, the glass-sponge, *Hyalonema* (cf. Fig. 198, p. 302).

(Drawn to different scales, by Charles Schwartz under direction of W. C. Curtis, from nature and from the sources noted.)

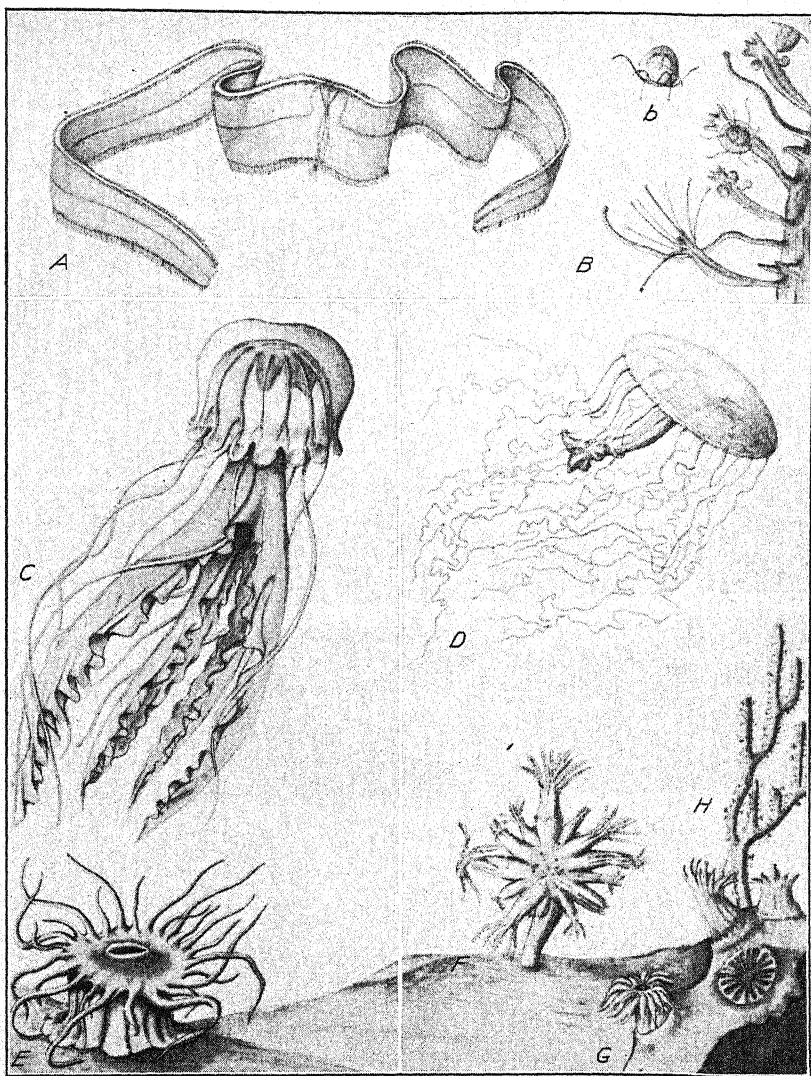


FIG. 138. Representative Coelenterata and Ctenophora. A, the ctenophore, *Cestus*, or "Venus' girdle" (after Chun). B, the hydroid colony, *Hydractinia carnea*, with its several types of polyps, including its medusæ, or jellyfish; b, one of these jellyfish after liberation (after Brooks). C, the jellyfish, *Pelagia cyanella* (after Agassiz). D, the jellyfish, *Eutima variabilis* (after Brooks). E, a sea-anemone, *Antheomorpha elegans* (after Hertwig). F, the sea-pen, *Renilla reniformis* (after Wilson). G, the North Atlantic coral, *Astrangia danae*. H, a "staghorn" coral.

(Drawn to different scales, by Charles Schwartz under direction of W. C. Curtis, from nature and from the sources noted.)

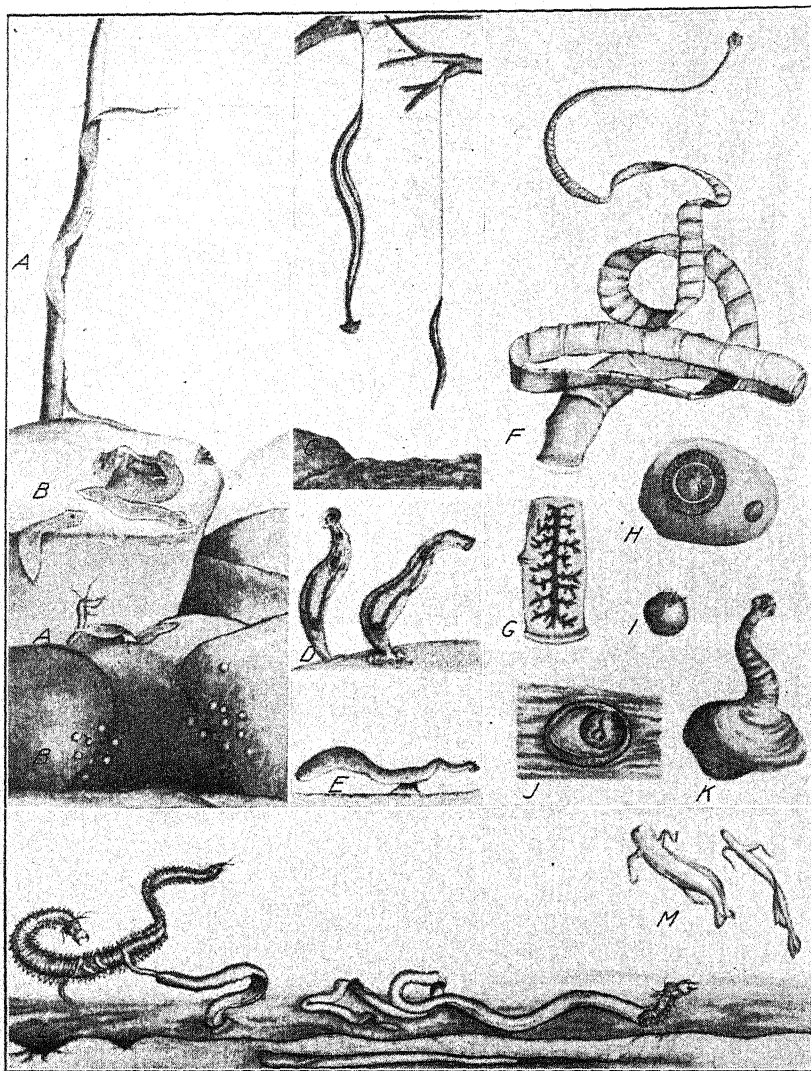


FIG. 139. Representative flatworms. A, fresh-water planarian, *Procotyla fluviatilis*, crawling upon water plant and attacking hydra. B, planarian, *Euplanaria novangliae* (*Planaria maculata*), crawling and feeding; egg capsules shown on stones below. C, land planarians, *Bipalium* and *Rhynchodemus* (after Bresslau). D, parasitic trematode, *Sphyranura osleri*, attached to surface of mud puppy, *Necturus*. E, parasitic trematode, *Gorgoderina*, attached within urinary bladder of frog. F-K, adult and stages in life-cycle of tapeworm, *Tænia solium*. L, burrowing nemertean, *Cerebratulus lacteus*, attacking clamworm. M, swimming nemertean, *Nectonemertes mirabilis*.

(Drawn to different scales, by Charles Schwartz under direction of W. C. Curtis, from nature and from the sources noted.)

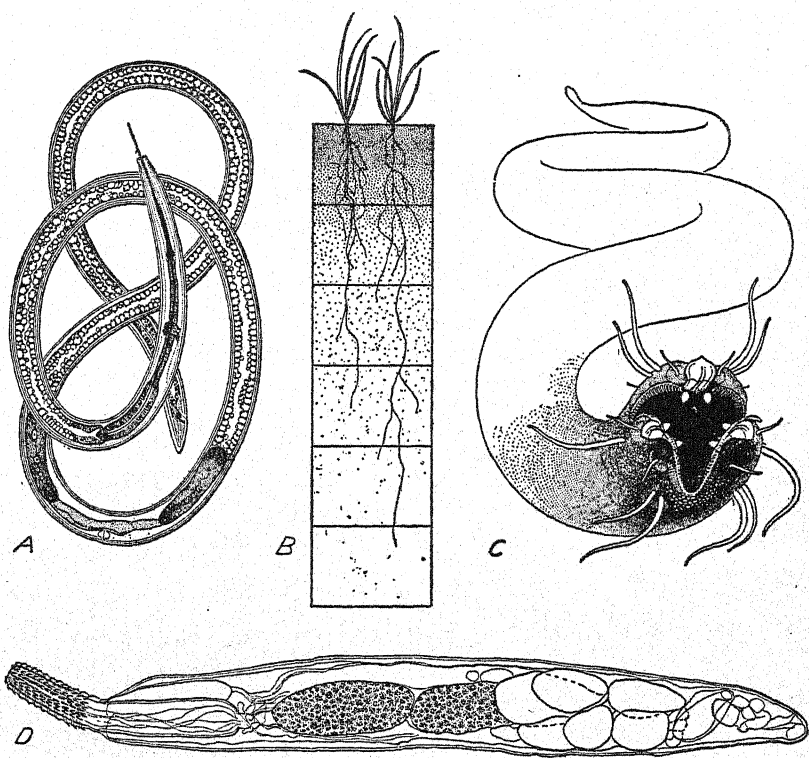


FIG. 140. Representative roundworms. *A*, the dagger nematode, *Xiphinema*, an injurious form, which coils itself about the rootlets of plants in such a way that the spearlike structure at the anterior end can be thrust far into the tissue of the rootlet upon which the worm feeds. *B*, diagram showing by stippling the relative abundance of nematodes of all kinds in each successive two inches of a low-lying alluvial soil estimated to contain three billion nematodes per acre; though shown distributed uniformly in each layer, the worms are really most numerous about the roots of plants. *C*, carnivorous nematode that feeds upon other nematodes. The three jawlike parts of the mouth are armed with teeth and the head has tentaclelike projections that are presumably sensory. *D*, one of the Acanthocephala, the spiny-headed worm, *Echinorhynchus dirus*, parasitic in the intestine of certain fishes, showing the proboscis armed with hooks, which serve for attachment to the host; the internal structures which consist almost wholly of reproductive organs are shown in optical section.

(*A*, *B*, and *C*, from N. A. Cobb, 1914, Yearbook U. S. Dept. Agriculture. *D*, from H. J. Van Cleave, 1931, Transactions American Microscopical Society, vol. 50. Drawn to different scales.)

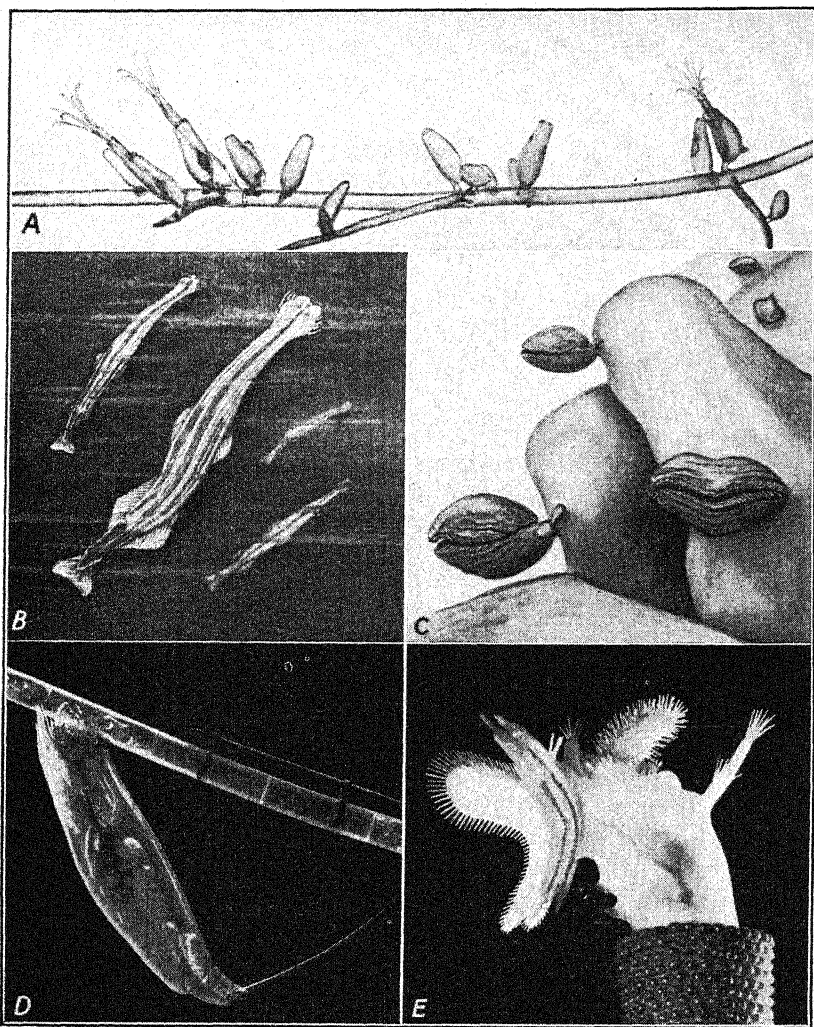


FIG. 141. Representatives of the phyla, Bryozoa, Chaetognatha, Brachiopoda, and of the class Rotatoria. A, several individuals of the marine bryozoan, *Bowerbankia gracilis*. B, the chaetognath, *Sagitta*. C, the brachiopod, *Terebratulina*. D, the rotifer, *Trichocerca longiseta*, feeding upon the plant *Spirogyra* by boring through the cell walls. E, the tube-building rotifer, *Floscularia ringens*, protruding from its tube, which is composed of spherical particles cemented together.

(Bryozoan and rotifers from Roy W. Miner, 1925, *Natural History*, vol. 25. Courtesy author and American Museum of Natural History. *Sagitta* and *Terebratulina* from drawings by Charles Schwartz. Reproduced to different scales.)

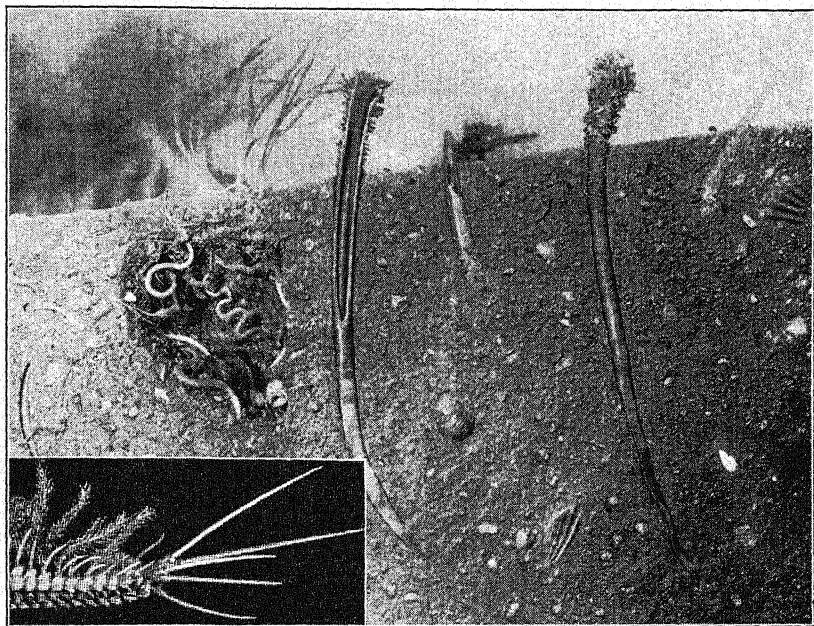
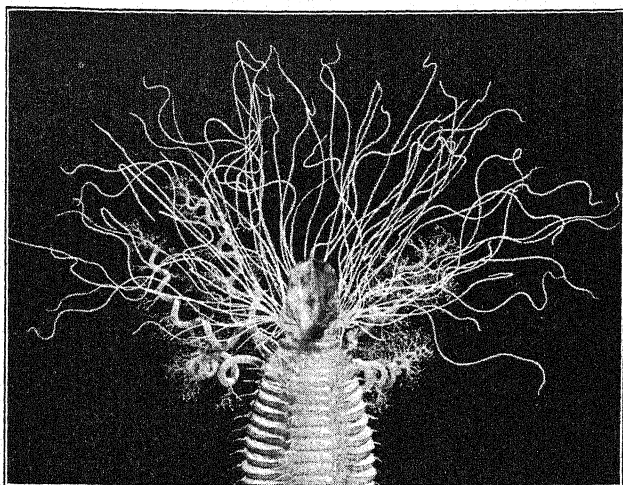


FIG. 142. Representative Annelida. *Above*, anterior end of a marine tube-worm, *Amphitrite ornata*. *Below*, burrowing sea-worms: *left to right*, the wormlike chordate, *Dolichoglossus* (cf. Fig. 431, p. 587); the plumed worm, *Diopatra cupræa*, in its long, leathery tube, which is shown cut open and also intact; and the tubeworm *Pectinaria* (*Cistenides*), which lives head downward in a tube constructed of sand grains cemented together. *Inset*, the anterior end of the plumed worm.

(From Roy W. Miner, 1925, *Natural History*, vol. 25. Courtesy author and American Museum of Natural History. Reproduced to different scales.)

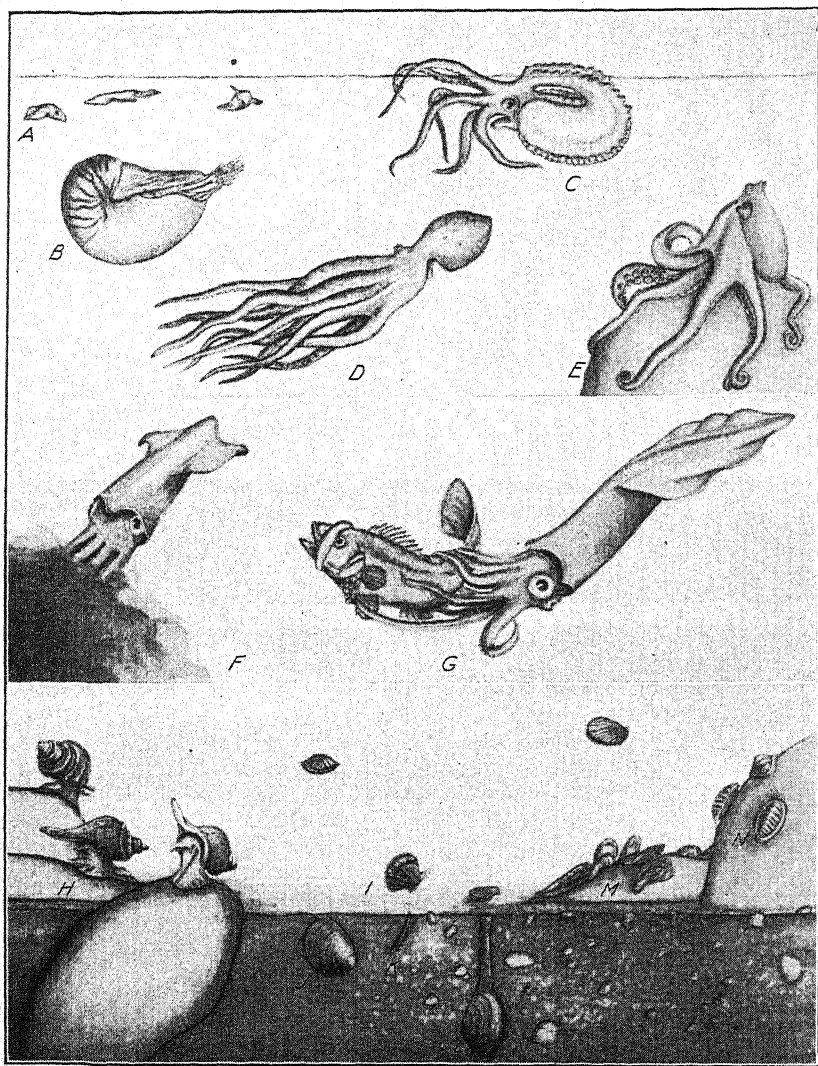


FIG. 143. Representative Mollusca. A, young squids, *Loligo pealei*, swimming near surface. B, "pearly nautilus," *Nautilus pompilius*, in swimming position (after Griffin). C, "paper nautilus," *Argonauta argo*, floating at surface. D, "devil fish," *Octopus*, swimming. E, "devil fish," at rest. F, squid, *Loligo*, discharging cloud of ink. G, squid, *Loligo*, capturing prey. H, snails, *Busycon canaliculatum*, crawling. I, scallops, *Pecten irradians*. J, hard-shell clam, *Venus mercenaria*. K, "tooth-shell," *Dentalium*. L, soft-shell clam, *Mya arenaria*. M, oysters, *Ostrea*. N, "armadillo snails," *Chitopileura*.

(Drawn to different scales, by Charles Schwartz under direction of W. C. Curtis, from nature and from the sources noted.)

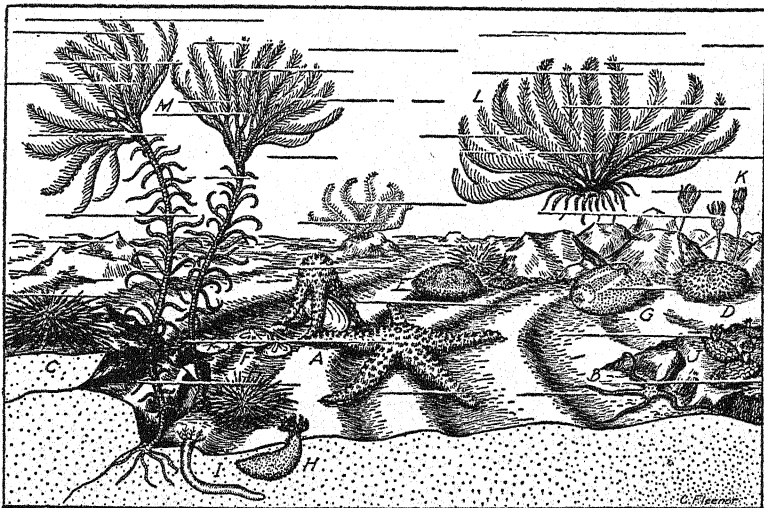


FIG. 144. Representative Echinodermata; shown in their orientation with respect to the substratum, without reference to the depths at which they live. A, two individuals of *Asterias*, an asteroid; one of them feeding upon a clam. B, *Ophiura*, an ophiuroid. C, *Arbacia*; D, *Strongylocentrotus*; E, *Clypeaster*; F, *Echinarachnius*; and G, *Spatangus*: echinoids; only the tests of *Echinarachnius* and *Spatangus* are shown, the latter with its oral surface uppermost. H, *Thyone*; I, *Leptosynapta*; and J, *Psolus*: holothurians. K, young, attached individuals of *Antedon*; L, adult, free-living *Antedon*; and M, *Metacrinus*: crinoids.

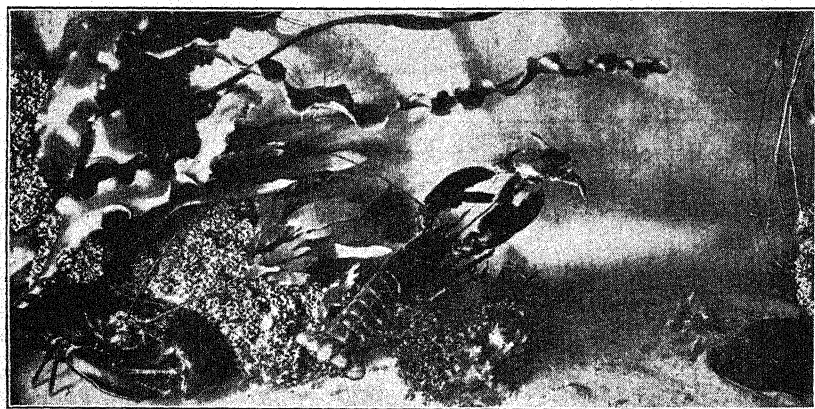
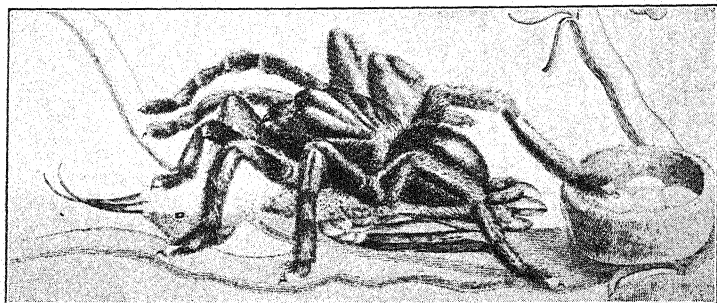
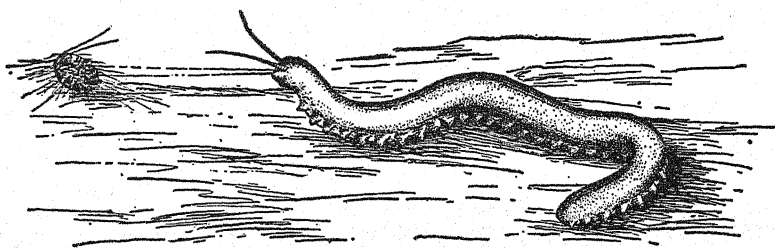


FIG. 145. Representative Arthropoda: Onychophora, Arachnida, and Crustacea. *Above*, the onychophoran, *Peripatus*, in its defensive reaction, entangling a cockroach in sticky threads discharged from two papillæ beneath the head. *Middle*, a large tropical spider, an arachnid, devouring a humming bird, as described by Madame Merian, in 1705, and confirmed by recent observers, after being questioned for many years. *Below*, crustaceans, lobsters on ocean bottom, one of them lying in wait in its crevasse between the boulders, the other capturing a crab, another crustacean.

(*Above*, from A. S. Pearse, "General zoölogy," copyright, 1917, Henry Holt and Co., reprinted by permission. *Middle and below*, from E. W. Gudger and Roy W. Miner, respectively, 1925, Natural History, vol. 25. Courtesy authors and American Museum of Natural History.)

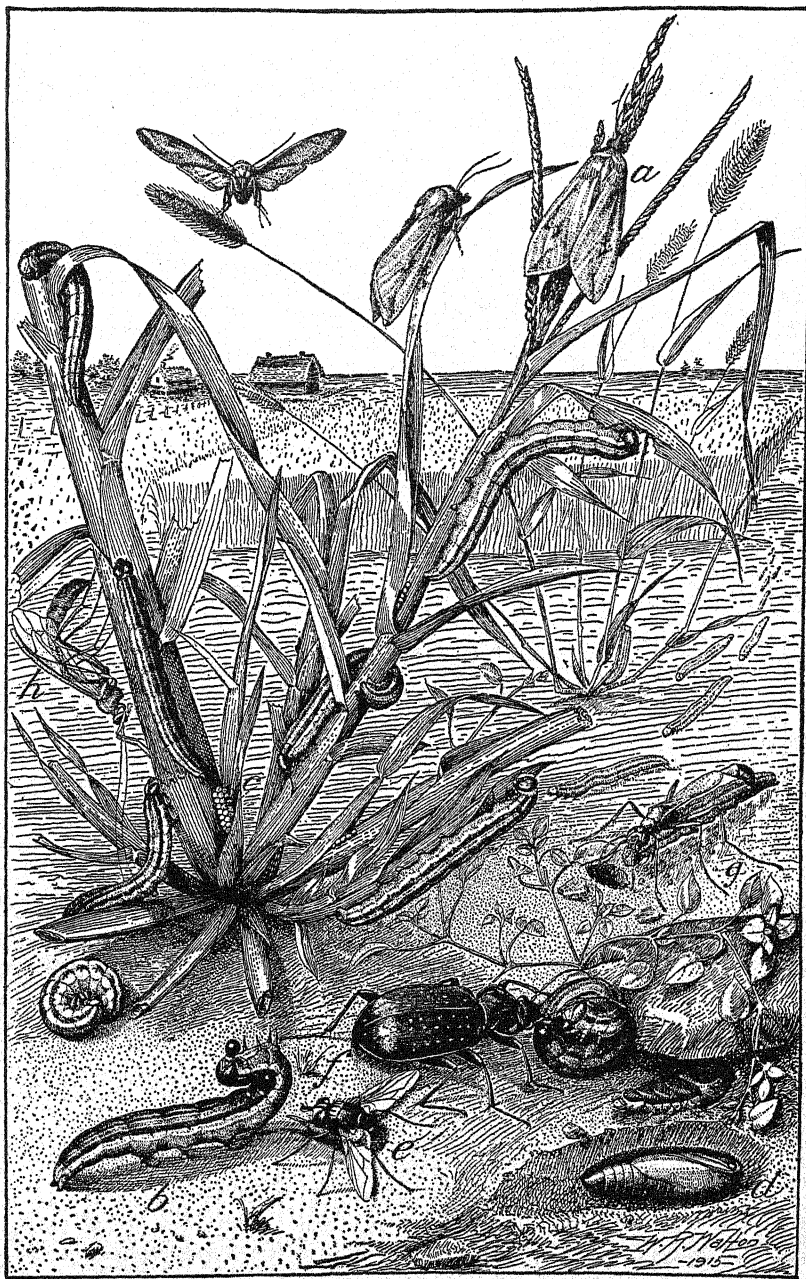


FIG. 146. Representative Arthropoda : Insecta. A study in ecology : the life-cycle and relationships to other species of the true army-worm, *Cirphis unipuncta*, one of the Order Lepidoptera. *a*, parent or adult moth; *b*, full-grown larva; *c*, eggs; *d*, pupa in soil; *e*, parasitic fly, *Winthemia quadripustulata*, laying its eggs on an army-worm; *f*, a ground beetle, *Calosoma calidum*, preying upon an army-worm, and, at right, *Calosoma* larva emerging from its burrow; *g*, a digger wasp, *Spheca* sp., carrying an army-worm to its burrow; *h*, *Enicospilus purgatus*, an ichneumon-fly parasitic on the larva of the army-worm. All about natural size.

(From W. R. Walton, 1916, Farmers' Bulletin, No. 731, U. S. Dept. Agriculture.)

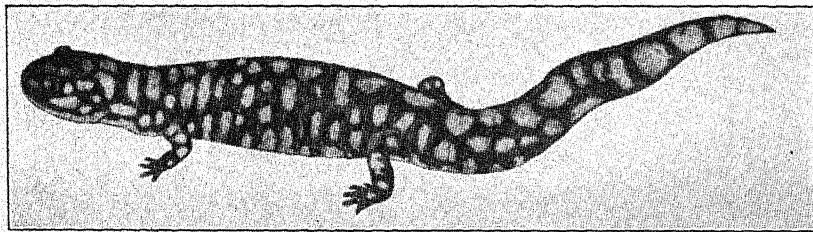
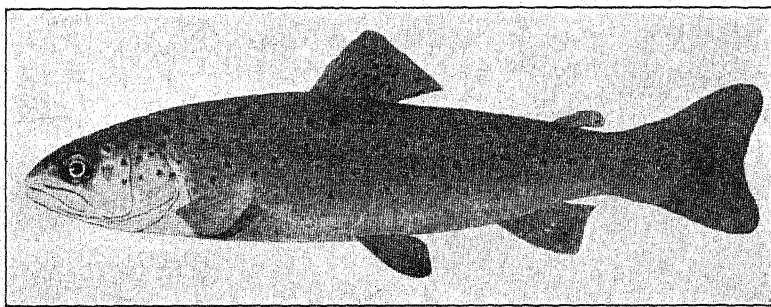
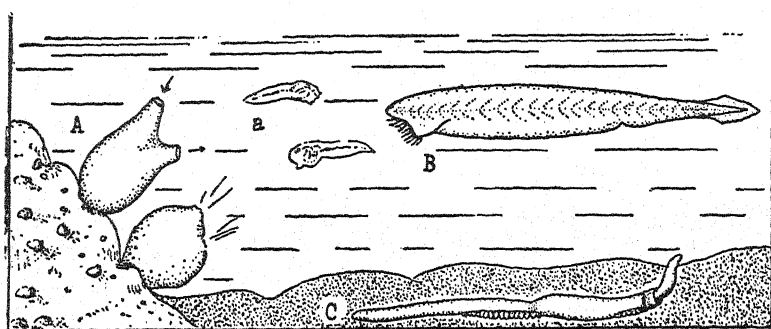


FIG. 147. Representative Chordata: marine, fresh-water, and land dwellers. Above, primitive chordates: A, a tunicate, and *a*, its larval stages on a much larger scale; B, the lancelet, *Branchiostoma* (*Amphioxus*), a cephalochordate; C, the "acorn worm," *Dolichoglossus* (*Balanoglossus*), a hemichordate (cf. Fig. 431, p. 587). Middle, a bony fish, the brown trout, *Salmo fario*. Below, an amphibian, the tiger salamander, *Amblystoma tigrinum*.

(Middle and Below, from Report New Jersey State Museum, 1906, after Agassiz and Holbrook, respectively.)

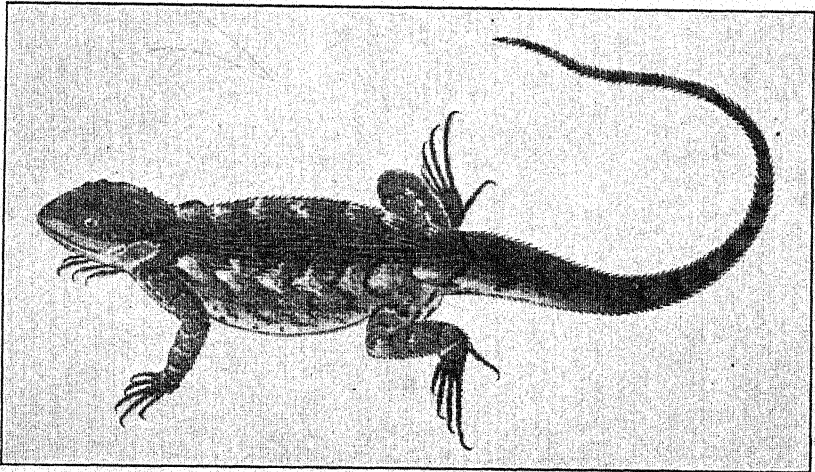


FIG. 148. Representative Chordata: bird and reptile. *Above*, wild ducks, representative of wide-ranging birds. *Below*, the pine-tree lizard, *Sceloporus undulatus*, a representative reptile.

(*Above*, from sketch by Charles Schwartz. *Below*, from Report New Jersey State Museum, 1906, after Holbrook.)

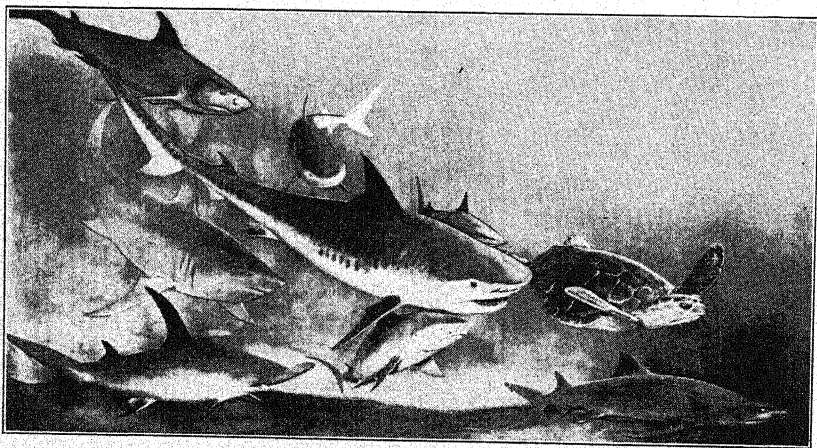
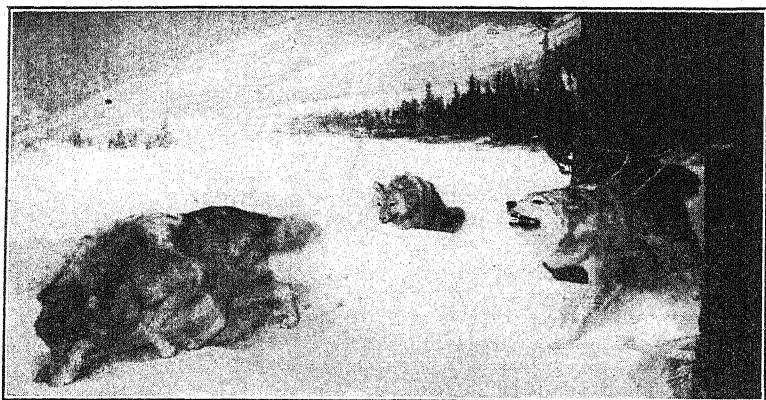


FIG. 149. Representative Chordata: wolves of the land and sea. *Above*, timber wolves on the trail. *Below*, sharks pursuing a sea turtle.
(Photographs of group exhibits in the American Museum of Natural History. Courtesy of the Museum.)

In this manner the phyla may be grouped into larger subdivisions according to a classification that seems justifiable to many zoölogists. How the principal phyla may be divided into classes has been shown by Figure 134. It should be realized, however, that any classification merely represents an opinion of experts which is based upon the knowledge available at a given time. There may be differences of opinion among the experts, even when the same data are involved. Many details and many general aspects of classification must remain matters of judgment unless more explicit evidence is forthcoming than any now available. Yet there has come to be an increasing degree of agreement as knowledge of animal life has progressed.

Aristotle classified animals into those with red blood and those without such blood. Early in the nineteenth century the great anatomist Cuvier (Fig. 470, Left, p. 648) divided the Animal Kingdom into four main types: *Vertebrata*, *Articulata*, *Mollusca*, and *Radiata* or *Zoöphyta*. With increasing knowledge, however, it was seen that each of these types included forms so diverse that they should not be placed in a single animal group. Notable examples were the separation of Cuvier's *Articulata* into *Arthropoda* and *Vermes*, and the subsequent division of the *Vermes* into several phyla. Again, Cuvier's *Radiata* was subdivided into the Phylum *Echinodermata** and the Phylum *Cœlenterata*, and later the Phylum *Porifera* was separated from the *Cœlenterata*. More knowledge has made more phyla, although a limit is reached in such groups as the *Chordata*, *Arthropoda*, *Mollusca*, and *Echinodermata*, with their clearly defined characteristics.

The term *invertebrate* should be explained before proceeding, since it is one that may be confusing despite the fact that *invertebrate* obviously means a *non-vertebrate* animal. It is often convenient to speak of the invertebrates in contrast to the vertebrates. The vertebrates include the most familiar forms of animal life. Moreover, their complexity and the fact that man is a vertebrate make us think of them as standing apart from the remainder of the Animal Kingdom. Although this distinction is convenient, it is an artificial one from the standpoint of classification. It cuts through the Phylum *Chordata*, some members of which are vertebrates and some invertebrates. It is thus in contrast with the distinctions between the phyla or the distinction between *Protozoa* and *Metazoa* (cf. Fig. 135).

The Basis and Meaning of Classification. The evolutionary aspects of classification may now be examined. The basis for modern classifications is structure, and structural resemblances are believed to indicate evolutionary relationships. When it is said that certain ani-

mals are chordates, or cœlenterates, or annelids, it is meant that the animals of such a group are more akin to one another than to any other group. Hence, the natural or genetic classification, which zoölogists have constructed upon the basis of structural resemblance, is an attempt to construct a family tree of animal life. If certain phyla are placed together as Eumetazoa, the grouping means that they are regarded as closely related in ancestry. It is, therefore, possible to regard such a classification as the one under discussion as a *statement of evolutionary probabilities*.

Referring to Figure 135 as though it were a family tree, one may say that the first great step in the evolution of animals was the divergence between forms that continued in a unicellular state and gave rise to the Protozoa, and forms that acquired the many-celled state and gave rise to the Metazoa. Within the latter line, the next great divergence was between forms that continued in a primitive state without a gut cavity, the Mesozoa and Parazoa, whose surviving descendants are the Phyla Mesozoa and Porifera, respectively; and forms that acquired a gut cavity, along with other complexities, and became the Eumetazoa, whose descendants are all the remaining phyla. Next came a divergence into two stems: one of them, the Radiata, with radial symmetry, and another, the Bilateria, with bilateral symmetry. Again, within the great stem Bilateria, there came to be forms with and without a body cavity, and this body cavity became specialized in various ways. And, finally, we have come in the course of evolution to the existing phyla with their subdivisions until the species and the individual animals are reached.

The table of life-cycles may be consulted in this connection (Fig. 194, p. 293). Thus it can be shown how Metazoa may have arisen from a unicellular ancestry in common with Protozoa, and how the existence of a unicellular stage in the life-cycle of every many-celled animal that reproduces by syngamy may be regarded as a persistent ancestral condition. The fact that many members of the phyla grouped as Bilateria exhibit the so-called gastrula stage in their development (*cf.* Figs. 83 and 283, pp. 141 and 394) has been taken to mean that a two-layered condition, which Radiata and Bilateria have both inherited from their common eumetazoan ancestry, now persists in the adult cœlenterates and ctenophores and as a developmental stage in many existing Bilateria. The gastrula is a two-layered sac, comparable with the cœlenterate type of structure, whatever may be its evolutionary significance. The argument from the particular facts of the gastrula stage is like the argument from the fishlike stages in the development of the higher

vertebrates (*cf.* Fig. 89, p. 148) and from various stages of development within other phyla which are suggestive of ancestry. According to such an interpretation, the frog arises from male and female gametes, which form a zygote that develops through gastrula and fishlike stages, because it has not lost these evidences of its evolutionary history as a

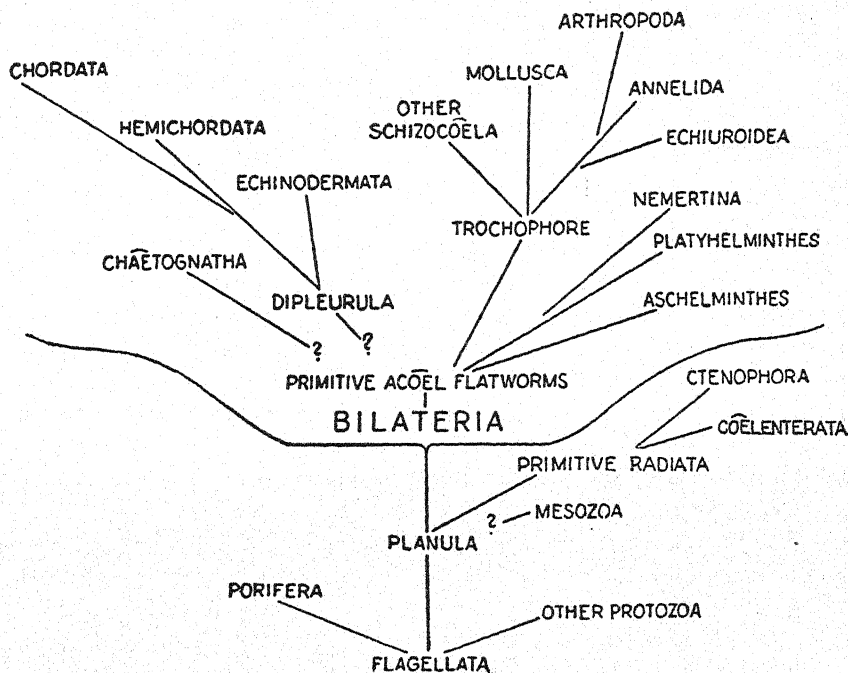


FIG. 150. Hypothetical tree of the evolutionary relationships of animal groups (*cf.* Fig. 135).

(Modified from Libbie H. Hyman, "The invertebrates: Protozoa through Ctenophora," copyright, 1940, by McGraw-Hill Book Co., reprinted by permission.)

metazoan and a vertebrate (*cf.* p. 681). Classification upon a basis of structure is therefore more important than mere cataloging because it is fundamentally the study of evolution as well (*cf.* p. 671).

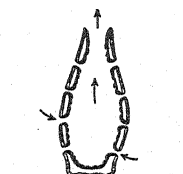
Thus, *the grand course of evolution* can be pictured if one speculates upon the changes that have occurred since animals became differentiated from plants. It is clear that the major steps in this great drama occurred at a very early period, because the earliest sedimentary rocks that contain an abundance of fossils show representatives of all the great phyla except the Chordata (*cf.* Fig. 469, p. 646). Although such conclusions regarding major evolutionary changes are frankly specula-

tive, they are based upon facts of structure observed in existing animals and interpreted in the manner shown. The conclusions here drawn may be represented more graphically by the family tree shown as Figure 150.

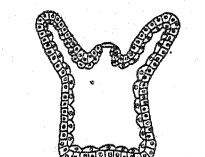
Organization of the Animal Body

Forms of Symmetry. The body plans of animals fall into a few general types (Figs. 151 and 152). With respect to symmetry, some protozoans and many sponges are *asymmetrical*; they have no geometrical regularity of organization, since there are no planes that will divide them into comparable parts. A few protozoans are *universally symmetrical*; the body is spherical, and many planes can be drawn through the center of the sphere that will divide the animal into symmetrical halves (Fig. 152). Such animals as the jellyfishes and hydroids are *radially symmetrical*; like a cylinder, the body can be divided into many symmetrical halves by planes drawn through a central axis. In addition the body of such an animal shows a *polarity* whereby the two ends of the cylinder have different structures and functions; there is a *polar axis* extending from mouth to base, or from mouth to anus if there is an anal opening. Animals such as the sea-anemone (Fig. 152) exhibit a symmetry that seems to have arisen by an evolution from radial symmetry through specialization of opposite sides of the body; only two planes will divide the individual into symmetrical halves. Thus, an approach to bilateral symmetry is suggested, although the organization is not properly comparable with the bilaterality of higher animals and is better called *biradial symmetry*. The great majority of animals are *bilaterally symmetrical*; only one plane will divide them into symmetrical parts. These animals have *anterior*, or "head," ends and *posterior*, or "tail" ends; they have *dorsal* or "back" and *ventral* or "belly" surfaces. However, most of these bilateral animals show a degree of asymmetry in some of their parts, as do the frog and other vertebrates in which the skeletal, nervous, and voluntary muscle systems are strictly bilateral, whereas the digestive and circulatory systems are noticeably asymmetrical.

Each of these forms of symmetry is associated with a mode of life. Animals with universal symmetry float freely in water. Asymmetrical animals are usually attached and encrusting forms. Radially symmetrical animals are attached at the basal end with the mouth or comparable parts at the opposite or oral end; if free-living, like the jellyfishes and starfishes, these radial forms have probably come from ancestors that were attached and hence radially symmetrical. Bilaterally symmetrical animals are typically active and free-living, going

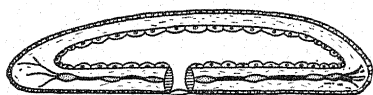


Parazoa

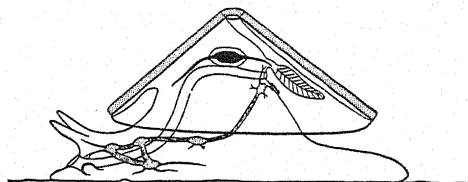


Radiata

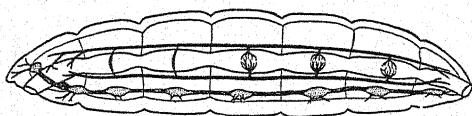
*Cœlenterata and
Ctenophora
Diploblastic
Radial*



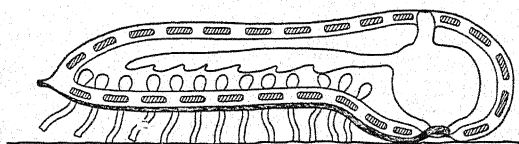
*Platyhelminthes
Triploblastic
Acoelomate
Non-metameric
Bilateral*



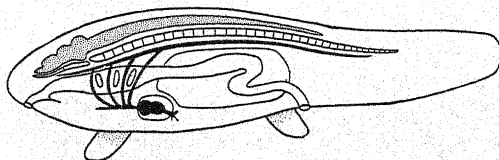
*Mollusca
Triploblastic
Coelomate
Non-metameric
Bilateral*



*Annelida
Triploblastic
Coelomate
Metameric
Bilateral*



*Echinodermata
Triploblastic
Coelomate
Non-metameric
Radial*



*Chordata
Triploblastic
Coelomate
Metameric
Bilateral*

FIG. 151. Types of structure in major phyla of the Animal Kingdom.

"head end first" in the familiar fashion. Some bilateral animals, which live attached or in a fixed position, show an arrangement of their bilateral parts that approaches radial symmetry; these forms give

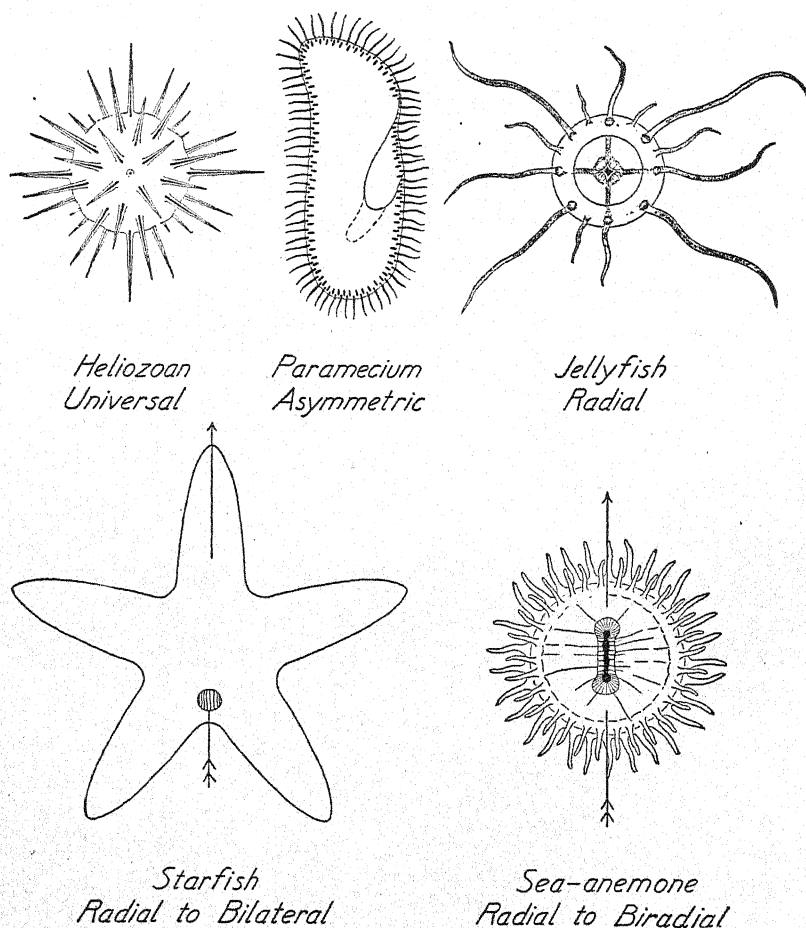


FIG. 152. Forms of symmetry in animals. The familiar bilateral type is not represented here.

further support to the generalization that radial symmetry is typically associated with attachment. From an evolutionary standpoint it is supposed that the ancestors of such bilateral attached animals were free living, that they became attached, and that they are now becoming somewhat radial as an adjustment to their attached mode of life.

Other Modes of Differentiation. In addition to being organized according to types of symmetry, animals may show *proximal* and *distal*

differentiations, as in attached forms where the base or proximal end differs from the distal or free end (Fig. 211, p. 316). In other cases there is an *oral* surface, which is differentiated from an *aboral*, as in a jellyfish or a starfish (Fig. 397, p. 537). Such proximo-distal and oral-aboral modifications are typical for radially symmetrical animals. Bilateral animals, on the other hand, exhibit *dorso-ventral* differentiation and *antero-posterior* differentiation. *Metamerism*, or the segmental differentiation that appears so clearly in the earthworm and other Annelida (Fig. 332, p. 449), is also characteristic of the Arthropoda and Chordata, as evidenced by the abdomen of a crayfish (Fig. 345, p. 469) and the vertebral column and ribs of a vertebrate.

Homology and Analogy. In making any classification that is based upon structure it is necessary to distinguish between the structural resemblance called *homology* and the functional resemblance called *analogy*. The fore limbs of reptiles, birds, and mammals are *homologous* whatever their functions, because all are constructed upon the same plan (cf. Figs. 487 and 488, pp. 668 and 669). They may or may not be *analogous*, since fore limbs have different functions, like the wings of birds, the flippers of whales, the front legs of horses, and the arms of men. The wings of a bird and those of an insect are analogous since they have the same function, but not homologous because they differ completely in structure. Again, the skeletons of insects and vertebrates are analogous but not homologous. Such comparisons are involved in evolutionary problems as well as in classification, because structural resemblance is taken to mean evolutionary relationship.

CHAPTER 8

UNICELLULAR ANIMALS: THE PROTOZOA

In Chapter 7 it was stated that the simplest animals are unicellular and are classified as the Phylum *Protozoa*, which may be contrasted with all the phyla of multicellular animals, or *Metazoa*. The Protozoa are defined as single-celled animals, although some protozoan cells are so highly organized that they far exceed the complexity of any metazoan cell, and although some protozoans are cell colonies. The word Protozoa, which means "first" or "primordial" animals, is well chosen, because the members of the Phylum Protozoa come first when animals are arranged in the order of complexity. Moreover, there are reasons for supposing that the Protozoa have descended, without changing their single-celled state, from the primeval organisms that were also the ancestors of the Metazoa. The phylum is divided into two subphyla: the Subphylum *Plasmodroma*, which includes the Class *Sarcodina*, the Class *Mastigophora*, and the Class *Sporozoa*; and the Subphylum *Ciliophora*, which includes the most complex protozoans, along with many simpler types, in the Class *Ciliata* and the Class *Suctorina*.

Although the vast majority of the Protozoa are free-living, all members of the Class Sporozoa are parasitic, and there are many cases of parasitism within the other classes. Some of these, such as the malaria parasite, cause serious diseases in man and domestic animals. Since the Protozoa are unicellular, they are of microscopic size save in exceptional species. Hence, they were not clearly distinguished in classification until about 1861, after cells were recognized as masses of protoplasm each containing a nucleus. Certain of the ciliates were observed by Leeuwenhoek as early as 1675, and many protozoans were described during the eighteenth and the first half of the nineteenth centuries. In this period before their cellular organization was known, the Protozoa were variously classified with many-celled animals, and a corresponding complexity was ascribed to some species. It is now known that ciliates, for example, do not have stomachs, hearts, and similar organs, as was once supposed, although some members of this class are surprisingly complex organisms.

The structural complexity that Protozoa exhibit is notable because it is within the limits of a single cell. The cells of multicellular animals are physiologically unbalanced, since they are specialized to carry on particular functions or closely related functions; they can exist in such a state of specialization because the many-celled organism taken as a whole is a physiologically balanced unit. The single cell constituting a protozoan necessarily performs all functions, and hence it must be physiologically balanced whatever its structural complexity. This physiological balance, which enables the protozoan to be a complete and independent individual, together with the complexity of many protozoan cells, has led some zoölogists to regard the Protozoa as animals to which the cell concept does not apply. Those who hold this view regard the Protozoa as a group of *acellular* animals to be compared with Metazoa only as individual with individual.

Their minute size and soft bodies have made it impossible for most types of Protozoa to leave any record as fossils. The groups known as Foraminifera and Radiolaria, which have limy and siliceous skeletons, respectively, are found abundantly in some of the very early fossil-bearing rocks and in subsequent marine deposits. Again, because of their minute size there are no commonly known forms of protozoans, although many persons have heard of the amœba, of the malaria parasite, and of the trypanosome that causes African sleeping sickness. In this chapter the Protozoa will be examined as a phylum of the Animal Kingdom and as animals whose unicellular organization may be contrasted with the multicellular organization described for the vertebrates. Also, the capacities of metabolism, irritability, and reproduction, which are characteristic of all protoplasm, will be examined and compared in the protozoan and the vertebrate.

The Sarcodina

In the Class *Sarcodina* are included the simplest forms of Protozoa, although the Mastigophora as a group seem to be the more primitive from an evolutionary standpoint. A distinctive feature of the Sarcodina is the capacity to form extensions of the cell body, called *Pseudopodia*, or "false feet," which are more or less temporary. In the Subdivision Rhizopoda, which includes creeping forms such as *Amœba* (Fig. 153 A), the pseudopodia are lobed or rootlike, sometimes subdividing, and may frequently change their shape or be withdrawn. In the Actinopoda, which are floating forms such as *Actinophrys* (Fig. 154), the processes are stiff and more permanent. The name Sarcodina was originally applied because protozoans of this class resemble

the flesh, or "sarcode," as the protoplasm of animal cells was first called. Notable among the Sarcodina is the Genus *Amœba* and related genera which are collectively termed amœbæ or amœbas.

The Amœba: General Structure. The protoplasm of an amœba (Fig. 155) consists of a thin external layer the *plasmalemma*, which

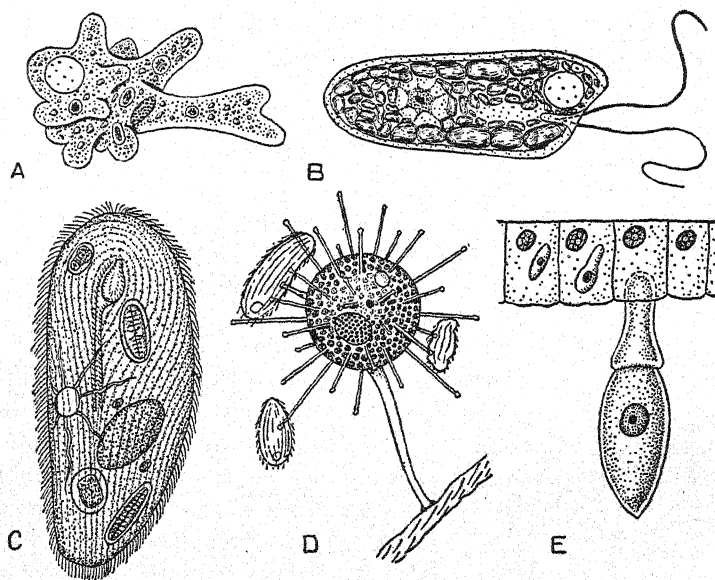


FIG. 153. Representative Protozoa. *A*, *Amœba*, Class Sarcodina. *B*, *Chilomonas*, Class Mastigophora. *C*, *Frontonia*, Class Ciliata. *D*, *Podophrya*, feeding on small ciliates, Class Suctorina. *E*, *Gregarina*, attached to an epithelial cell of host's intestine and stages in the life-cycle within other similar cells of host, Class Sporozoa.

(Drawn by Wiley Crawford.)

functions as the cell membrane; a non-granular region, the *ectoplasm*; and a granular inner region, the *endoplasm*, in which the nucleus is located. Features characteristic of cells and of protoplasm are thus apparent. The larger bodies distributed in the cytosome are *granules* of various sizes, the *food vacuoles* in which digestion occurs, a single *contractile vacuole*, other *vacuoles* containing watery fluid and comparable with those found in many cells, *crystals* of definite forms which may be distinctive for particular species of amœbæ and may occur in vacuoles, *oil globules*, and many small *inclusions* ranging to the limit of microscopic visibility. The significance of these parts will be discussed as necessary in the accounts that follow.

Movements and Irritability. The manner in which an amœba moves by the flowing of its irregularly shaped body has attracted attention ever since the animal was studied by the early microscopists, who called it the "proteus animalcule," or "changing little animal." This *amœboid movement*, which appears to be simple when first observed, is difficult to explain when further examined. Some of its features can be imitated by an inanimate object, such as a drop of

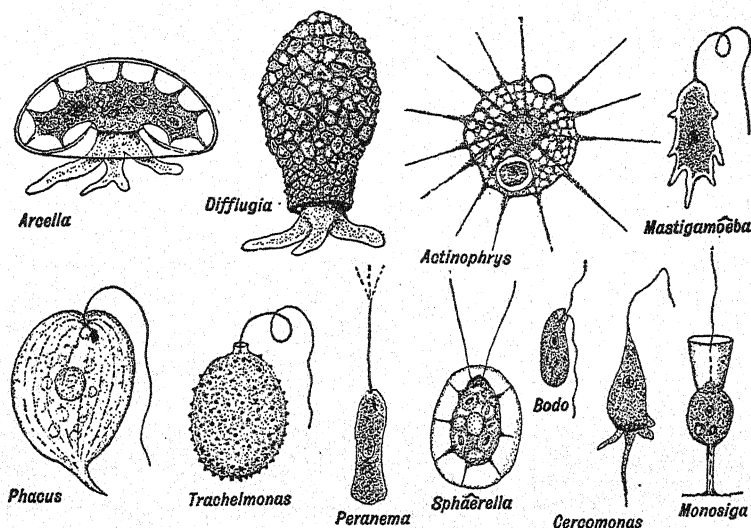


FIG. 154. Representative Sarcodina (*upper row*) and Mastigophora (*lower row*). *Mastigamœba*, which has a flagellum and pseudopodia, is classified as a mastigophoran.

(Drawn by C. E. Wilson.)

clove oil in a mixture of glycerin and alcohol or a drop of glycerin containing soot particles and placed in lubricating oil. But it is clear that the movements of such non-living bodies are not strictly comparable with the movements of an amœba, as once claimed. Various accounts have been given of the changes to be observed in the formation of pseudopodia and in the locomotion of different species. Thus, amœbas have been described as extending their pseudopodia like jets of water from a fountain, with a current flowing outward in the center and backward on all sides; they have been described as rolling like a sac with an elastic wall and fluid contents; and they have been described, and photographed from a side view, as "walking" upon stiff pseudopodia (Fig. 156). According to a recent account, some large amœbas move by contraction of the ectoplasm and flowing of the

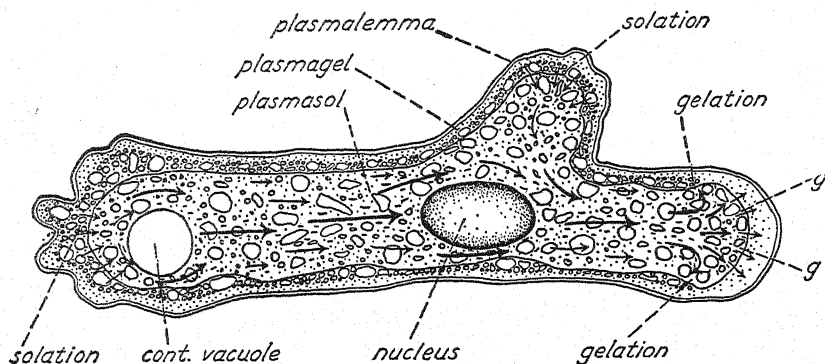


FIG. 155. Structure and locomotion in *Amoeba*. The amoeba has an inner granule-containing fluid substance, the plasmasol, surrounded by a more solid layer of similar composition, the plasmagel, which are together equivalent to what is termed the endoplasm. Outside, there is a hyaline portion of the plasmagel, surrounded by the plasmalemma; these constitute the ectoplasm. During locomotion the plasmasol and plasmagel become transformed into one another after the manner shown in the figure; the plasmasol moves forward and at the end of the advancing pseudopodium becomes transformed into plasmagel, which in turn is becoming plasmasol at the posterior end. *g*, region of a sievelike gelation.

(After S. O. Mast, 1926, *Jour. Morphology and Physiology*, vol. 41.)

endoplasm, which changes from a sol or fluid state to a gel or gelatinous state, and from gel to sol. They progress as a tunnel might if the mortar of its wall became fluid at the posterior end and flowed within the tunnel to its anterior end, carrying the bricks to be laid again anteriorly by a new setting of the mortar (Fig. 155).

The movements and other reactions of an amoeba in response to stimuli, or changes in the environment, make up the behavior in this unicellular animal in the same manner as the collective reflexes make

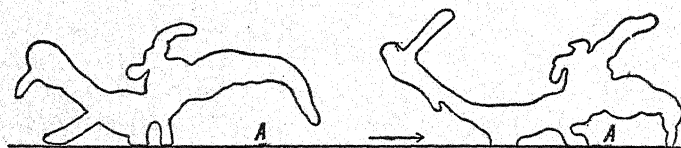


FIG. 156. Outlines of successive stages in the movements of a single amoeba as seen laterally. Such "walking" upon the pseudopodia, which can flow out and be retracted, is apparently a method of locomotion in some species. *A* marks a fixed point on the surface.

(Outlined from the photographs by O. P. Dellinger, 1906, *Jour. Experimental Zoölogy*, vol. 3.)

up the behavior of multicellular organisms such as vertebrates (*cf.* p. 74). One can compare the activities of the single cell composing an amœba with those of a white blood cell in the human body (*cf.* p. 98), or one can think of the amœba as an individual animal to be compared with another individual. In the former case one compares cell with cell, and the parallels are obvious. In the latter comparison one forgets about the cellular organization and thinks only of the individual as a

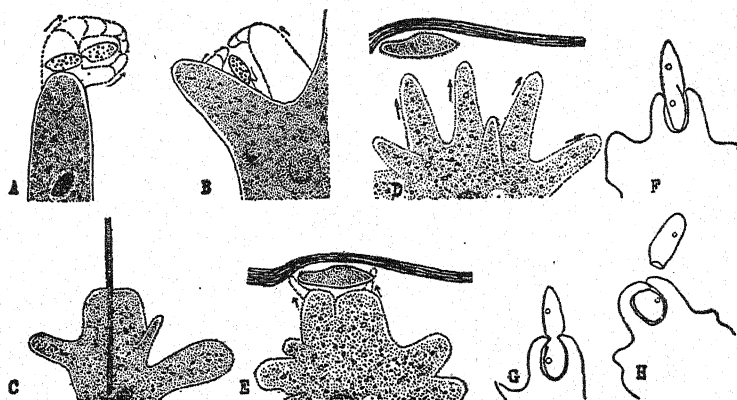


FIG. 157. Feeding reactions of amoebas. *A* and *B*, ingesting motile prey, such as small flagellates, by means of pseudopodia and formation of large food vacuoles; the dotted lines indicate successive positions of the pseudopodia and the prey. *C*, ingesting non-motile prey, a filamentous alga, without the formation of a food vacuole. *D* and *E*, "cornering" a paramecium against a bit of debris. *F*, *G*, and *H*, cutting a paramecium into two pieces.

(*A* and *B*, modified from W. A. Kepner and W. H. Taliaferro, 1913, *Biological Bulletin*, vol. 24; *C-E*, from W. A. Kepner and W. C. Whitlock, 1921, *Jour. Experimental Zoölogy*, vol. 32; *F-H*, from Mast and Root, *Jour. Experimental Zoölogy*, vol. 21.)

whole. Thus, the behavior of the white blood cells when they move into certain regions and ingest such foreign bodies as bacteria may be compared with the behavior of amœbas. The behavior of other cells in the vertebrate animal may be similarly compared, although the parallel is not so evident.

Thoughtful consideration of an amœba as an individual reacting to its environment and in comparison with another individual, such as the many-celled vertebrate, enables one to recognize broad factors common to each and to state them in general terms irrespective of the cellular organization in either animal. Despite this comparison of individual with individual, what is called the behavior of an amœba is based upon the capacity of irritability as shown by the protoplasm of a single independent cell. The behavior of a multicellular animal is

likewise based upon the irritability of cells, but such behavior involves reactions in sequence by a number of cells.

Most reactions of amoebas that can be easily demonstrated are negative, since they consist in withdrawals of pseudopodia or contractions of the cell in response to stimulation (Fig. 159). Positive reactions

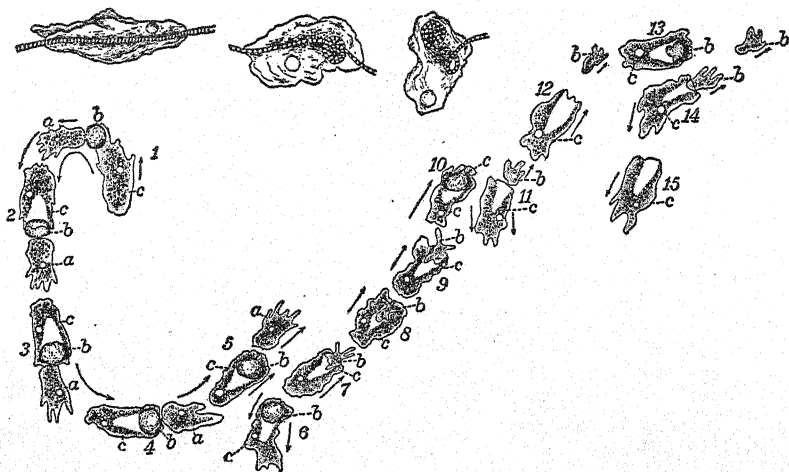


FIG. 158. Feeding reactions of amoebas. Above, *Amoeba verrucosa* ingesting and coiling within its protoplasm a filament of the plant *Oscillaria*. The absence of a vacuole surrounding the food in its early stages is characteristic for the ingestion of motionless food bodies. Below, pursuit, capture, and ingestion of one amoeba by another; escape of the captured amoeba and its recapture; final escape. The observer had attempted to cut an amoeba into two pieces with the tip of a fine glass rod. The posterior third of the animal, in the form of a wrinkled ball (b), remained attached by a slender cord and the larger part of the animal (a) began to flow, dragging this ball. A larger amoeba (c), approaching at right angles, came in contact with b, turned, and followed. Note the escape of a at 5, and the final escape of b.

(From H. S. Jennings, "Behavior of the lower organisms," copyright, 1906, by Columbia University Press, reprinted by permission.)

tions are seen in certain responses to contact and in feeding (Figs. 157 and 158). Thus, an amoeba that is dropped into water and settles slowly toward the bottom through a considerable distance may give a positive response by extending pseudopodia in all directions. If one of these pseudopodia comes in contact with a surface, for example, the stem of a water plant or the bottom, the amoeba may respond positively by flowing in this direction and may thus begin to move over the surface. If one of its pseudopodia is then touched with a glass rod or if cer-

tain chemical compounds in solution are brought in contact with a pseudopodium by means of a capillary pipette, a negative response may be indicated by withdrawal of the pseudopodium or by contraction of the entire amœba into a globular form if the stimulus is sufficient.

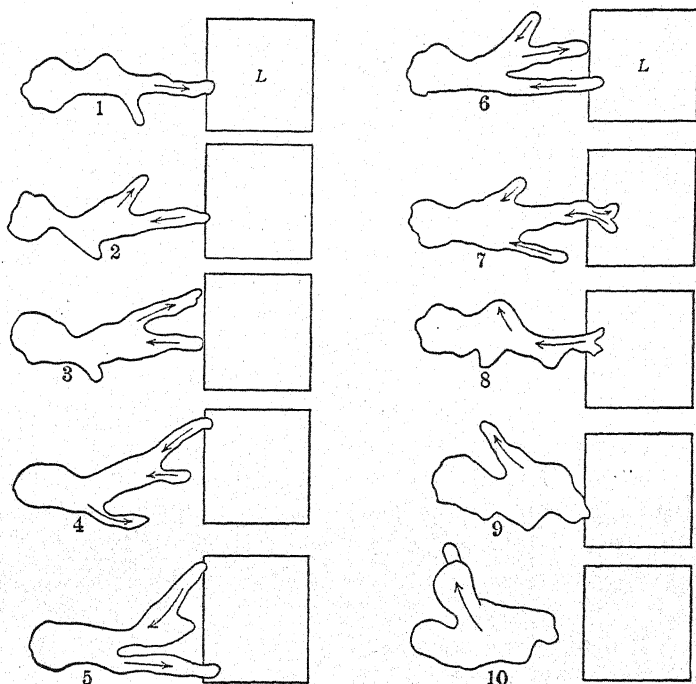


FIG. 159. Reactions of an amœba proceeding toward an area of intense light, the rays of which were perpendicular to the slide. *L*, field of light formed by focusing the light upon the slide. 1-10, successive positions of the amœba a little less than one-half minute apart. Arrows indicate direction of streaming in pseudopods.

(From S. O. Mast, "Light and the behavior of organisms," John Wiley & Sons, copyright, 1911, by author, reprinted by permission.)

Positive reactions seen in feeding will be described in the account of metabolism that follows.

Feeding and Metabolism. Amœbas feed upon other organisms, both animals and plants (Figs. 157 and 158). Such a species as *A. proteus* is essentially a beast of prey, eating whatever it can capture from small to relatively large protozoans and single-celled plants. It may even feed upon small many-celled forms. However, the most common food of this species consists of small flagellates and ciliates,

which may be consumed at the rate of fifty to one hundred daily. *Ingestion* consists typically in the formation upon the surface of the amoeba of a cuplike depression, which closes upon the prey and is then transferred to the endoplasm. In this manner a *food vacuole* originates by the enclosure of a drop of water containing one or more food bodies. The feeding reactions are complex and variable. Forms such as motionless unicellular plants call forth responses different from those induced by active prey. A form that the amoeba digests readily may be selected, while another form that is relatively indigestible by this amoeba is rejected, although both forms may be present in equal numbers. Moreover, the responses are not fixed but vary with the physiological state of the amoeba. In the adjustment of reaction to stimulus and to the state of its protoplasm the behavior of an amoeba resembles that of multicellular animals.

The resemblances between the metabolic processes in an amoeba and a vertebrate may be shown by tracing the history of the ingested food (Fig. 160). When a small flagellate, such as *Chilomonas*, is ingested by *A. proteus*, the prey moves about for several minutes before it becomes motionless and is killed by something within the vacuole. Meanwhile, the vacuole, which contains at the outset a relatively large amount of water, shrinks by diffusion of the excess water into the cytoplasm, and the remaining fluid becomes alkaline. In later stages the reaction of the vacuole becomes acid. If the changes in individual vacuoles are followed, the *Chilomonas* will be seen to disintegrate gradually until, some 12 to 24 hours later, there remain only certain granules that are apparently indigestible. Fat globules are liberated from the food mass and appear in the fluid of the vacuole within 2 or 3 hours, after which they gradually decrease in size until they disappear. Starch grains disintegrate into a pasty mass, which disappears as the vacuole slowly decreases in volume.

The disintegration of other particles and further shrinkage of the vacuole follow, until only a few granules remain; and even these remnants may pass into the protoplasm instead of being egested. *Egestion* occurs by the discharge of food in various stages of digestion and of the indigestible residue that remains when all the digested material has passed into the cytoplasm. Often several vacuoles in late stages coalesce, and the mass comes in contact with the plasmalemma at or near the posterior end of the amoeba to be egested by rupture of this membrane. From such observations it is inferred that fats, carbohydrates, and proteins are digested in the food vacuoles, presumably by enzymes as in the digestive tracts of many-celled animals, and

that the products of such digestion pass into the protoplasm as they pass into the cells lining a digestive tract. Or the comparison may be made with the nutrients that pass from the surrounding lymph to the cells in all parts of the vertebrate body. Thus, the digested food enters the protoplasmic system, where it is *assimilated* as in the cells of vertebrates and all other animals.

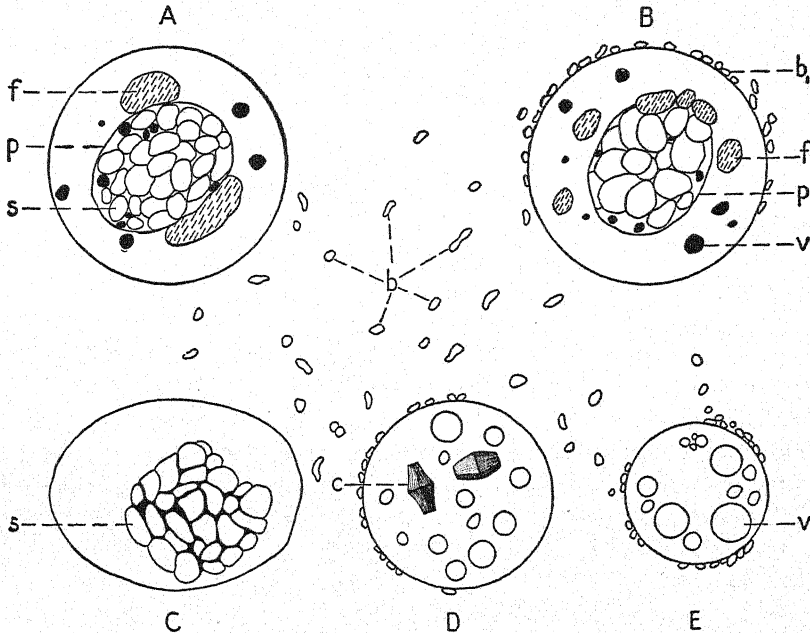


FIG. 160. Stages in the digestion of a flagellate protozoan, *Chilomonas* (cf. Fig. 153 B), within a food vacuole of *Amœba proteus*. A, 2-6 hrs.; B, 6-8 hrs.; C, 8-16 hrs.; D and E, 16-30 hrs.; b, granules free in the cytoplasm; b₁, granules in contact with food vacuole; f, fat; s, starch; v, refractive bodies in vacuoles; c, crystal; p, pellicle at surface of *Chilomonas*.

(Redrawn from Mast and Doyle, 1935, Arch. für Protistenkunde, vol. 86.)

Oxygen is necessary for the continued life of an amœba, as may be shown by placing amœbas in water from which the dissolved oxygen has been removed. Presumably, this oxygen enters from all parts of the cell surface in the same manner as oxygen enters the cells of a vertebrate from the intercellular lymph (cf. Fig. 18, p. 38). The respiration of *Amœba* is, therefore, comparable with the *internal respiration* of the vertebrate and likewise precedent to the reactions of *dissimilation*. This dissimilation by oxidation may in turn be compared with what has been described for vertebrates. The resulting products are carbon

dioxide, water, and nitrogenous compounds, which are removed from the protoplasm by *excretion* from the cell surface.

The function of the contractile vacuole in Protozoa appears to be the removal of excess water from the cell. Presumably, this water contains a certain amount of excretory material in solution; to this extent the contractile vacuole may be regarded as having an excretory function. The many species of Protozoa that have no contractile vacuoles must effect their excretion entirely from the general cell surface. Such a diffusion from the surface of the cell into the water by which the amoeba is surrounded is comparable with the excretion into the surrounding lymph from the cells of a vertebrate. It is thus apparent that the metabolic processes of this unicellular animal and the complex vertebrate are essentially similar. The fundamental requirements for assimilation and dissimilation within cells are everywhere comparable, although in each species the cell synthesizes the particular compounds characteristic of its protoplasm.

Life-cycle and Reproduction. The life-cycle, or life history, of a many-celled animal is the series of changes from egg to adult which occurs in each generation. Single-celled animals also exhibit serial changes which constitute their life-cycles. From what is known regarding other protozoan life-cycles, one might expect that an amoeba would reproduce asexually by various forms of *cell division* and perhaps sexually by *gametes* that would unite by a process of *syngamy* comparable with the union of gametes in metazoa (cf. p. 130). One might also look for a process of *encystment*, in which the amoeba would become globular and secrete a covering for protection or in connection with cell division within such a *cyst*. All these processes have been described for the common fresh-water amoebas, but until recently the difficulties in rearing amoebas in cultures have been such that the earlier accounts could not be checked effectively. Within the last few years improvements in technique have made it possible to maintain species, such as *A. proteus*, for many months under laboratory conditions and even to follow specimens individually. Observations upon such pedigreed cultures have disclosed nothing but an endless series of cell divisions by *binary fission* (Fig. 161). Cell division by the *budding* of small cells from a large one, by *multiple fission* to form many small cells, and *gamete formation* perhaps occur, but they have not been observed; and so doubt is cast upon the earlier accounts of these processes, although they may be observed eventually. For the present it is certain only that these amoebas reproduce by binary fission with subsequent growth of the cell to full size and continue indefinitely in the active state without syngamy.

or encystment. Modifications of these processes are that the amœba may become smaller through starvation or that the cytosome may fail to divide immediately after division of the nucleus, thus producing a multinucleate cell. Such divisions of the nuclei and growth of

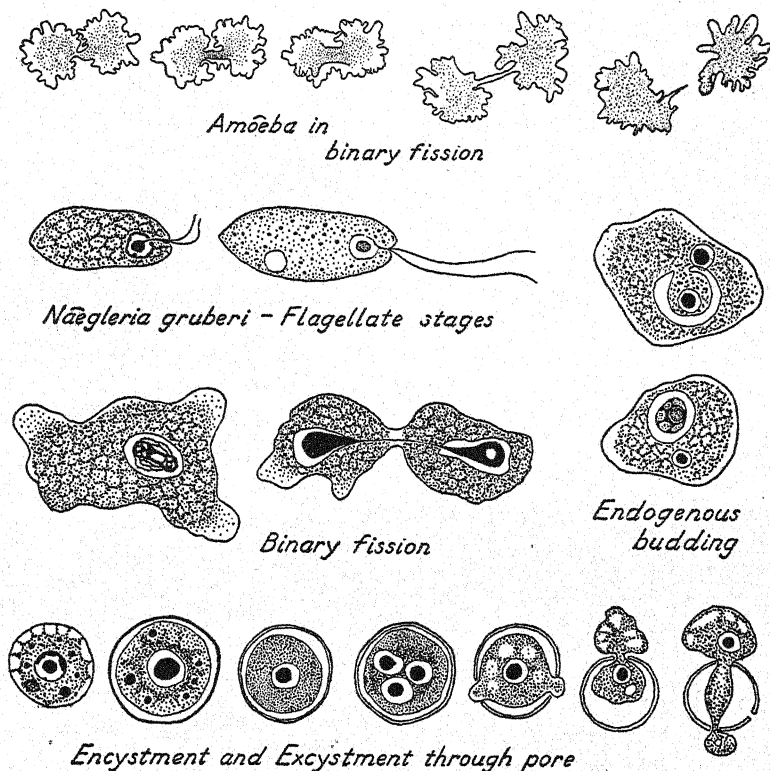


FIG. 161. Stages in the life-cycles of amoebas.

(*Amœba*, redrawn from E. F. Botsford, 1926, Jour. Experimental Zoölogy, vol. 45; *Nægleria*, redrawn from C. W. Wilson, 1916, Univ. of California Publications, vol. 16.)

the cytoplasm without division produce the *giant amœbas* which occur in the life-cycles of some species. Eventually, these multinucleate cells return to a mononucleate stage by the association of each nucleus with near-by cytoplasm to form a typical cell. It is true that more complex life-cycles with budding and encystment have been discovered in some of the other amoebas (Fig. 161), including flagellate stages, and cycles with gametes and syngamy are known for some of the Sarcodina.

Other Sarcodina. In the subdivision of the Sarcodina that is known as the *Rhizopoda*, there are many free-living forms that re-

semble the Genus *Amœba*. Also, many species of parasitic amœbas are found in the digestive tracts of other animals, particularly verte-

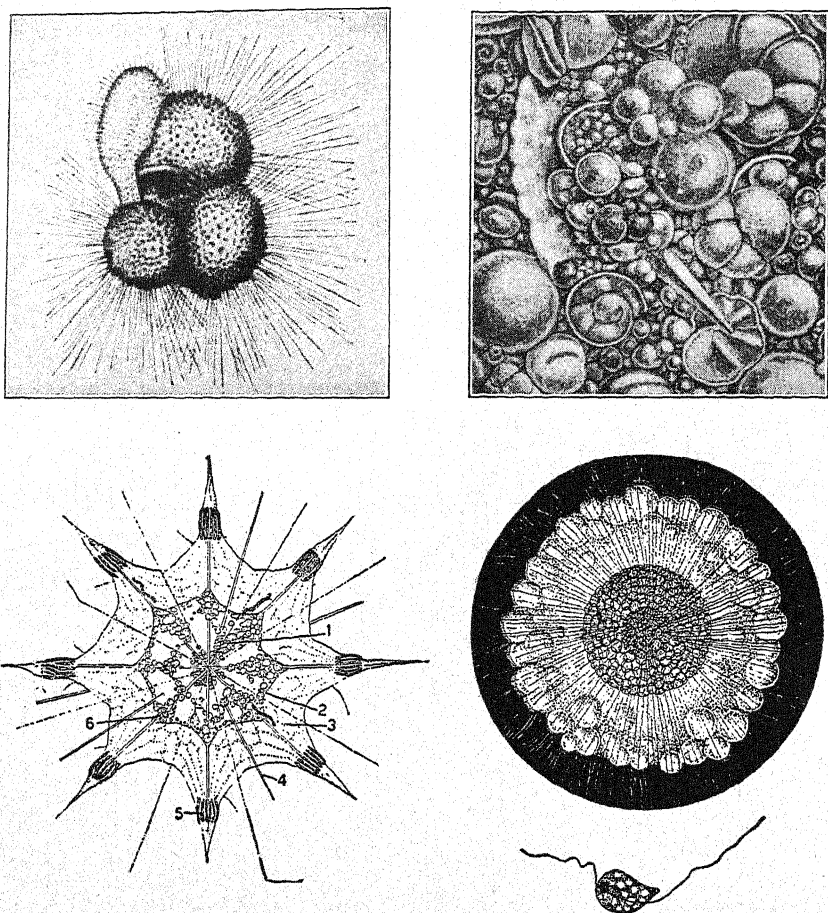


FIG. 162. Representative Foraminifera and Radiolaria. Above, left, the foraminiferan, *Globigerina sacculifera*; right, foraminiferal ooze from ocean bottom at depth of 11,000 feet. Below, left, the radiolarian, *Acanthometra*; right, *Thalassicola* and the biflagellate isogamete of a radiolarian.

(Above, left, from L. Rhumbler in W. Kükenthal, "Handbuch der Zoölogie"; right, from A. E. Shipley, "Zoölogy of the invertebrata," copyright, 1903, by A. and C. Black, reprinted by permission. Below, from Hyman, "The invertebrates: Protozoa through Ctenophora," copyright, 1940, by McGraw-Hill Book Co., reprinted by permission.)

brates; some of these cause serious diseases (cf. Figs. 187 and 188). Other rhizopods, such as the Genera *Arcella* and *Diffugia*, possess shells from the mouths of which issue pseudopodia and into which the

animals can withdraw (Fig. 154). In the *Foraminifera* there is a shell composed of carbonate of lime, chitin, silica, or other materials, and the pseudopodia pass through this shell by one or by numerous openings. With few exceptions the *Foraminifera* are marine, living near the surface of the ocean, as well as on the bottom. The shells of dead foraminiferans make up the greater part of the silt that occurs on the ocean floor in regions such as the deeper portions of the North Atlantic (Fig. 162). In chalk formations of various parts of the world, some of them hundreds of feet in thickness, these minute shells make up as much as 70 per cent of the deposit. Another subdivision, the *Actinopoda*, includes the "sun animalcules," such as *Actinophrys sol* (Fig. 154), and the *Radiolaria* (Fig. 162), which are notable for their siliceous skeletons. The occurrence in some of the oldest sedimentary rocks of *Foraminifera* and *Radiolaria* almost identical with present-day species indicates that these forms, and so perhaps many other Protozoa, have remained almost unchanged from the days of the earliest known fossils.

The Mastigophora

In the Class *Mastigophora*, which means the "whip-bearers," are included the protozoans that possess one or more flagella, or whiplike extensions of the cytoplasm, during the more representative phases of their life-cycles. These flagella are primarily organs of locomotion; in some species they also assist in feeding; and they often seem to have tactile functions. Flagella are found likewise in many species of *Sarcodina*, but only during limited periods of the life-cycle (*cf.* Fig. 161). In a similar manner amoeboid stages occur in the life-cycles of many *Mastigophora*. This existence of both flagellate and amoeboid stages in single species suggests a closer relationship between *Sarcodina* and *Mastigophora* than between any other two protozoan classes. The *Mastigophora* have also a close relationship with plants, since many of these flagellate Protozoa possess chlorophyll and are sometimes classified as unicellular plants instead of animals. Among such plantlike mastigophorans are species of the Genus *Euglena*.

The *Euglena*: General Structure. The account that follows is sufficiently general to be applicable to any one of several species of the Genus *Euglena* that are common in fresh water and likely to be available for laboratory study. A typical euglena (Fig. 163) is covered with the so-called *pellicle*, which is comparable with the cell wall in plant cells and is often marked externally with a spiral pattern. This

pellicle is stiff enough to preserve the contours of the organism as it swims through the water, but flexible enough to allow the changes of shape called euglenoid movement. When the euglena is viewed laterally, a mouthlike notch is seen in profile at the anterior end of the organism (Fig. 163). From this

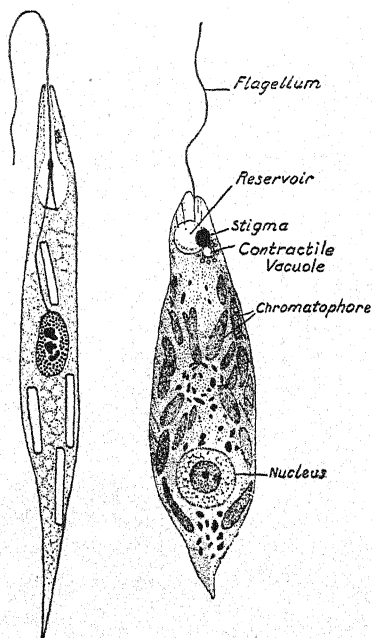


FIG. 163. Structure of *Euglena*. Left, *Euglena acus*, showing origin of flagellum within the cell. Right, *Euglena viridis*, showing other details.

(Left, from Hall and Jahn, 1929, Trans. American Microscopical Soc., vol. 48. Right, after F. Doflein, "Lehrbuch der Protozoenkunde," 1909, Fischer.)

opening a flask-shaped cavity extends a short distance into the cell. The single *flagellum*, which protrudes from this cavity, arises from two branches, one of them extending to the nucleus, and is composed of an *axial filament* surrounded by a *sheath*. In the euglena, this cavity from which the flagellum arises does not function as a mouth and gullet because the nutrition of the euglena is like that of green plants; in related flagellates which ingest and digest food these parts can be properly called a cell mouth and gullet. The term *organelle* is used for such cell "organs" as the flagellum and gullet. Periodically, in this anterior end of the cell, minute vacuoles enlarge and then coalesce to form a *contractile vacuole*, which discharges into the gullet. As in amœbas such vacuoles are supposed to eliminate an excess of water from the cell and incidentally any soluble excretory material which this discharged water may contain. A mass of red pigment at the anterior end is called the *stigma*, or *eye-spot* (Fig. 163),

because it seems to be an organelle that is sensitive to light. The *nucleus* lies near the center of the cell. The cytoplasm is crowded with *chromatophores*, containing the chlorophyl, which gives the organism its green color and is comparable with that of green-plant cells. The most conspicuous inclusions in the cytoplasm between these chromatophores are bodies having characteristic shapes in the various species of *Euglena* and composed of *paramylum*, a carbohydrate allied to starch. There is no flowing of the cytoplasm as in the amœba, al-

though the cytoplasm has a pasty consistency shown when the euglenoid cell changes its shape.

Movements and Irritability. Characteristic expansions and contractions of the cell, which occur when the euglena is not in active locomotion, are called *euglenoid* or *metabolic movements*. The common method of locomotion is that effected by the flagellum, which beats in

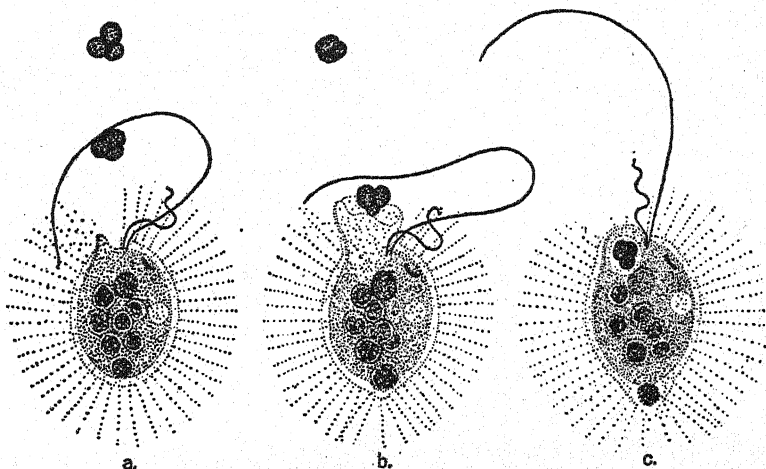


FIG. 164. Ingestion and egestion in the flagellate, *Monas vestita*. *a*, food particle brought toward the mouth region by the longer flagellum, the tip of which strikes the side of the body, thereby giving the initial stimulus for formation of food-cup. *b*, food being drawn into cup after having been brought nearer to cell by longer flagellum. *c*, ingestion completed and longer flagellum in position to repeat the process; fecal matter being egested at posterior end of cell. The dotted outlines represent a covering of what appears to be solidified mucus with numerous radiating threads.

(From B. D. Reynolds, 1934. *Arch. für Protistenkunde*, vol. 81.)

such a manner that the euglena is drawn through the water in a spiral course, rotating upon its long axis. Also, the euglena can crawl by spiral movements of the cell (Fig. 165).

By these movements of the cell body and by spiral swimming, the euglena reacts to a variety of stimuli. These reactions are collectively termed its *behavior*. The behavior with respect to light, which is a necessary factor in the environment of green euglenas, has been especially studied. For example, a euglena which has been crawling toward the source of light gradually changes its direction when the direction of the light is changed, and so again crawls toward the light. As Figure 165 shows, the adjustment involves a complex series of

movements including rotation of the cell upon its long axis, but once the orientation is completed, the euglena continues its spiral crawling in one direction. A similar positive response to light occurs in the free-swimming individual. In general, the euglena responds posi-

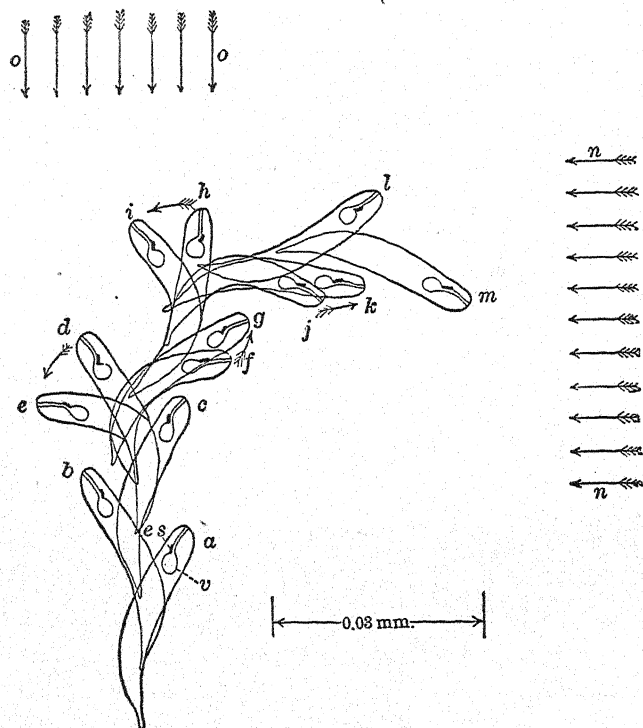


FIG. 165. *Euglena*, in crawling state, showing orientation with reference to light. *a-c*, positions of a euglena with light from *n* intercepted; *c-m*, positions after light from *n* is turned on and that from *o* turned off, thus changing direction of the light rays. *e s*, eye-spot; *n* and *o*, direction of light; *v*, contractile vacuole.

(From S. O. Mast, "Light and the behavior of organism," John Wiley & Sons, copyright, 1910, by author, reprinted by permission.)

tively to light of optimum intensity. If the light is very intense, the euglena may exhibit a negative response. In these and other reactions the euglenoid cell exhibits the irritability that is characteristic of all protoplasm.

Feeding and Metabolism. By virtue of its chlorophyll the euglena carries on the *holophytic nutrition* characteristic of green plants. The ingestion of small organisms through the gullet and thence into the

cytoplasm in food vacuoles has been described for euglenas but has not been confirmed by recent studies. As was previously stated, the gullet in the Genus *Euglena* is merely a flask-shaped cavity surrounding the base of the flagellum. However, such forms as *Peranema*, and other flagellates closely related to *Euglena*, ingest small organisms through a gullet and form food vacuoles, thus exhibiting the *holozoic nutrition* characteristic of most free-living protozoa (Fig. 164). When kept in total darkness, *Euglena gracilis* and certain other green flagellates lose their chlorophyll but live and multiply rapidly for long periods, if the kinds of chemical compounds necessary for the growth of molds

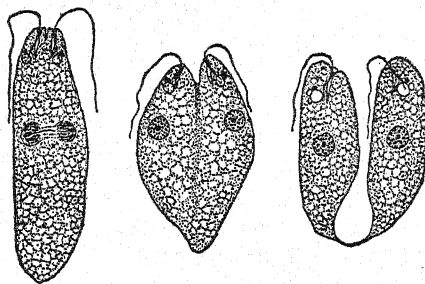


FIG. 166. Longitudinal fission in *Euglena gracilis*.

(From G. W. Tannreuther, 1923, Arch. für Entwicklungsmechanik, vol. 52.)

and fungi, as contrasted with green plants, are added to the medium. It is, therefore, established that the same species can maintain itself in sunlight by the *holophytic* nutrition of a green plant and in darkness by a *saprophytic* or *saprozoic* nutrition comparable with that of colorless plants. There are many species among these simple flagellates which thus combine holophytic and saprophytic nutrition. It is uncertain whether any single species is capable of all three types of nutrition, as was long claimed, erroneously, to be the case for the Genus *Euglena*.

Life-cycle and Reproduction. The life-cycle of euglenas, like that of amœbas, includes an *active phase*, during which the organism moves about, and an *encysted phase*, during which it is surrounded by a cyst and is non-motile (Fig. 167). Reproduction occurs by cell division, which is typically a longitudinal *binary fission* and may occur in either the active or the encysted phase of the cycle (Fig. 166). Reproduction by the *syngamy* of isogametes has been described for euglenas, but such observations were probably erroneous. So far as is known, there is no sexual reproduction in the flagellates that are most like the euglenas. Syngamy seems to occur in some of these simpler

flagellates (Fig. 168), and it is well known in colonial species of these protozoans such as *Eudorina* (cf. p. 290).

Other Mastigophora. The flagellate Protozoa are sometimes classified into two major groups, the animal-like and the plantlike Masti-

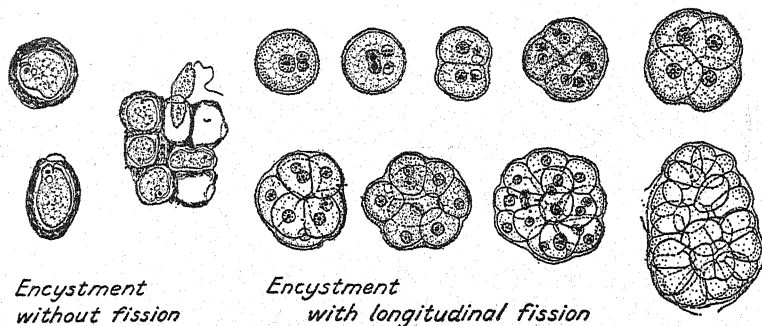


FIG. 167. Encystment in *Euglena gracilis*.

(From G. W. Tannreuther, 1923, Arch. für Entwicklungsmechanik, vol. 52.)

gophora. But the group is so heterogeneous that such a major subdivision has questionable value. It is clear that the mastigophorans are very difficult to separate from unicellular plants, on the one hand, and from the Sarcodina, on the other, and also from the Sporozoa, which are considered in the next section of this chapter. The class includes

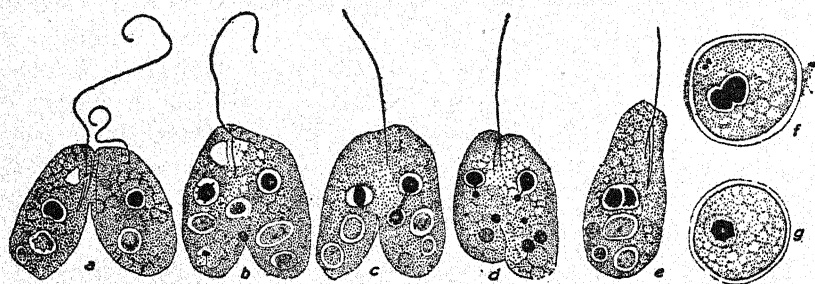


FIG. 168. Syngamy in the euglenoid, *Scytomonas subtilis*. *a* and *b*, fusion of the gametes; *c* and *d*, meiotic division of each nucleus; *e-g*, fusion of nuclei and cytosomes, and encystment.

(From V. Jollos in W. Kükenthal, "Handbuch der Zoölogie," 1923, vol. 1.)

many interesting forms. In *Mastigamœba* (Fig. 154), the cell is amœboid, although the presence of a flagellum leads to its classification as a mastigophoran. *Trachelomonas* (Fig. 154) has a firm pellicle and fixed shape. In *Peranema* (Fig. 154 and Fig. 136 B, p. 217)

the protoplasm is surprisingly mobile, and the flagellum can be held straight out, vibrating only at the end as the animal progresses, or it can be turned in any direction to explore the environment or redirect the course. In *Monosiga* (Fig. 154) and related forms there is a delicate collar surrounding the flagellum. *Noctiluca*, which emits light, is one of the organisms that produces luminescence in the ocean.

Many of the Mastigophora are parasitic. The posterior region of the digestive tract in man often harbors such forms, and almost any frog or tadpole will have more than one species of flagellate in its large intestine. The digestive tracts of termites disclose an amazing array of these protozoans. The forms called *trypanosomes* occur in the blood of vertebrates and in the digestive tracts of invertebrates (Fig. 189). These parasites are elongated cells with an undulating membrane along one side, on the edge of which is attached a flagellum that arises at the anterior end of the cell and becomes free posteriorly. A representative example is *Trypanosoma gambiense*, which causes one type of the sleeping sickness so fatal to man in equatorial Africa. Among the plantlike Mastigophora there are colonial species which suggest a transition from the unicellular to the multicellular state (cf. pp. 288-291).

The Sporozoa

The Class *Sporozoa* includes only parasitic species. In correlation with this mode of life the locomotor and other structures necessary in free-living animals are degenerate. The name Sporozoa, which means "seed-animals," was given because seedlike stages, or *spores*, are conspicuous in the life-cycles of these Protozoa. Representative examples are species of the Genus *Monocystis*, which inhabit the seminal vesicles of earthworms (Fig. 169). The full-grown individual is an elongated cell with a single nucleus. A slow locomotion is effected by local contractions and extensions of the cell, but there is no complexity of locomotor structures or behavior. The monocystis is first an intracellular parasite and later lies free in the fluid of the seminal vesicle. Presumably, the parasite absorbs its food over the entire surface of its cell body and eliminates any products of dissimilation in a similar manner. It stores in its cytoplasm an abundant reserve, which is used during the subsequent encystment and gamete formation. The parallel between a monocystis in the earthworm's seminal vesicles and any cell of an earthworm or higher animal surrounded by lymph is a close one (cf. Fig. 18, p. 38). It is assumed that the same kind of constructive and destructive metabolic changes occur within the cell in each

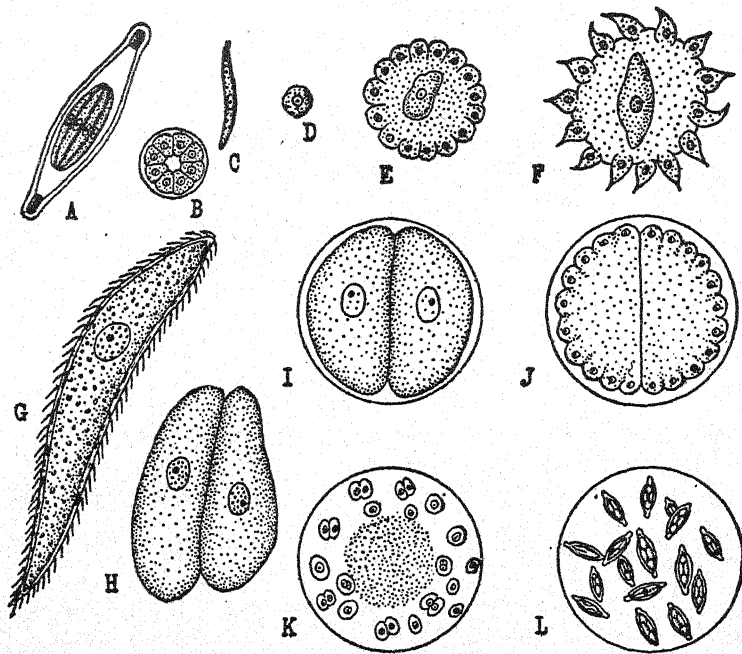


FIG. 169. Life-cycle of the sporozoan, *Monocystis*. A, spore consisting of a spore-case enclosing eight sporozoites. B, transverse section of same. C and D, liberated sporozoites. E, sporozoite after entering multicellular sperm-sphere of earthworm. F, growth in sperm-sphere to form a trophozoite, which is later surrounded (G) by the remains of the sperm-sphere, the tails of the spermatozoa resembling motionless cilia. H, two trophozoites that have become free of the degenerate sperm-spheres and united as gametocytes. I, encystment of gametocytes. J, reproduction by sporulation, or multiple division of the nucleus followed by cytosomal constrictions that form isogametes. K, reproduction by union of the isogametes to form zygotes; the residual cytoplasm of the gametocytes is in the center of the cyst. L, cyst containing many sporozoites, formed by secretion of a spindle-shaped spore case around each zygote, which then undergoes sporulation to form eight sporozoites; these eventually become arranged as in A and B, in which state they are transferred to another earthworm.

(Drawn by Wiley Crawford.)

case, and that income and outgo of material are comparable. The life-cycle is shown in Figure 169.

Other representative Sporozoa are the following: species of the Genus *Gregarina*, common in the digestive tracts of certain insects; the *coccidians*, which parasitize vertebrates and various invertebrate animals and of which the Genus *Eimeria* (Fig. 170) is representative; and the *malaria parasites* (cf. p. 279 and Fig. 186).

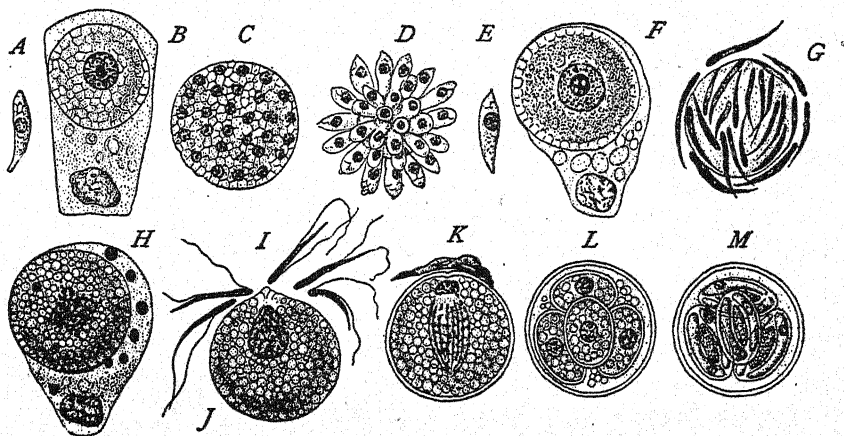


FIG. 170. Life-cycle of the sporozoan, *Eimeria* (*Coccidium*) *schubergi*. A, sporozoite. B, the full-grown eimeria in a gut cell of its host. C and D, asexual reproduction by cell division. E, gametocyte. F, immature macrogamete. G, microgametes. H, mature macrogamete. I and J, syngamy. K, zygote, forming cyst and showing microgametes that did not unite with the macrogamete.

L and M, cell division to form sporozoites within this cyst.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

The Ciliata

Many species of the Class *Ciliata* are complex and highly specialized cells far exceeding any cell specialization to be found in metazoans. A feature that is unique and almost universal is the separation of the nuclear material into two parts, a larger macronucleus and one or more smaller micronuclei, presumably with important differences in function. The other distinctive feature of these protozoans is their cilia. The Genus *Paramecium* is representative and includes species that have been the subject of many investigations.

The Paramecium: General Structure. If any forms can be called the omnipresent protozoans of fresh water, they are *Paramecium*

aurelia and *P. caudatum*, since no species of large size occur more commonly in cultures and under a wider range of conditions (cf. Fig. 171). Moreover, these two species can be easily maintained under laboratory conditions and are favorable for study. The account that follows deals with *P. caudatum*, unless otherwise stated. The size of the individuals seen in mixed cultures varies greatly, because, like other species of animals that have been exhaustively studied, the species is composed of many races which breed true among themselves but may differ widely when one race is compared with another (cf. Fig. 521, p. 716). Reproduction, food, and environmental factors also influence the size. The body is spindle-shaped with the anterior end bluntly rounded and the posterior end more pointed. At one side a depression, the *oral* or *buccal groove*, passes diagonally from the anterior end to about the middle of the body and ends in a *gullet*. *Cilia* clothe the body and are of uniform length, save at the posterior tip and in the oral groove, where they are slightly longer. Within the gullet, there is a special arrangement of the cilia.¹ Just posterior to the buccal groove is the *anal spot*, where egestion occurs.

The outermost layer of the cell is a thin elastic *cuticle* or *pellicle*, which shows under high magnification a geometric pattern related to the regular distribution of the *cilia* and *trichocysts* (Fig. 171). Beneath the pellicle is the *ectoplasm*, from which the cilia and trichocysts originate. The trichocysts, which are found in many other ciliated protozoans, are structures of problematic function. In the paramecium they are regarded as defensive parts, because upon stimulation they become long threads (Fig. 136 F, p. 217, and Fig. 180). The greater part of the cell is composed of the *endoplasm*, which is sufficiently fluid to allow circulation of its food vacuoles and movement of other particles. Since the endoplasm is thus fluid, it is the cuticle and ectoplasm which give the paramecium its definite shape. Within the endoplasm lie the *macronucleus*, which is related to the metabolic activities of the cell, and the *miconucleus*, which is related to heredity and reproduction. *Paramecium calkinsi* (Fig. 171) and *P. aurelia* have two micronuclei. The endoplasm also contains two *contractile vacuoles* with radiating canals and the *food vacuoles*. Larger masses of various sorts may also be found, in addition to the very small inclusions of the cytoplasm.

Movements and Irritability. Locomotion in *Paramecium* is effected by the cilia, which drive the animal in a spiral course like that of *Euglena* (Fig. 173). The factors involved in movement of this sort

¹ These cilia of the gullet are often called an *undulating membrane*. They are really what is called a *penniculus* by protozoologists.

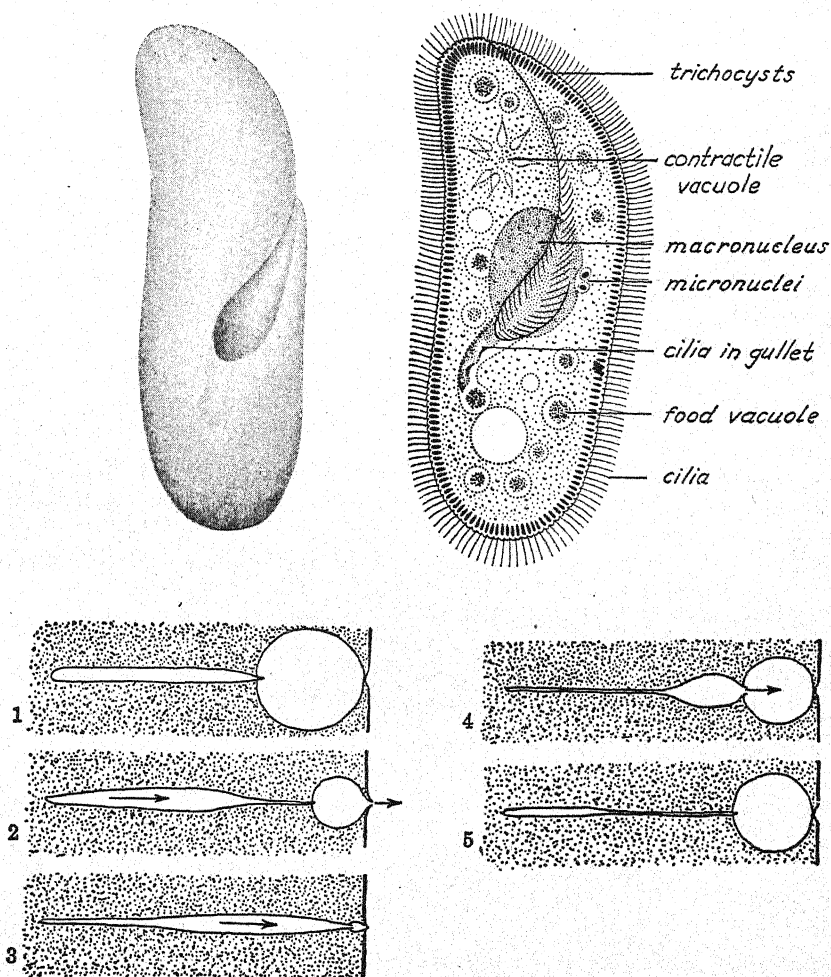


FIG. 171. Above, *Paramecium calkinsi*; left, external contours, showing oral groove leading to gullet, cilia and surface markings omitted; right, internal structure. Below, schematic representation of the emptying and refilling of contractile vacuole of a paramecium; only one of the radiating canals is shown.

(Above, from L. L. Woodruff, 1921, Biological Bulletin, vol. 41. Below, from W. Stempel, "Zoölogie im Grundriss," 1926.)

are *progression*, *rotation*, and a *swerving* of the anterior end. The animal moves forward, rotating on its long axis so that its oral surface is kept facing the axis of the spiral along which it is progressing. The presence of the last-named factor, the swerving aborally, results in a spiral instead of movement like that of a rifle bullet. The various locomotor reactions of the animal are conditioned by combinations and modifications of the three factors, progression, rotation, and swerving.

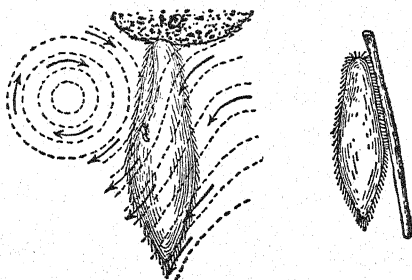


FIG. 172. *Paramecium* at rest. *Left*, against a mass of debris; the cilia are in active motion and are producing currents as shown by arrows. *Right*, at rest against a cotton fiber; the cilia in contact with the fiber are motionless, and the others are moving slowly, except those in oral groove, which remain active.

(From H. S. Jennings, "Behavior of the lower organisms," copyright, 1906, by Columbia University Press, reprinted by permission.)

For example, if a paramecium is swimming forward and comes in contact with a chemical solution that stimulates the cell strongly but does not injure it, the animal reverses its course and may swim backward spirally a considerable distance before the normal progression is resumed. The more common response, however, is that called the *avoiding reaction*, which is given to lesser stimuli, such as striking an obstacle (Fig. 174 A). In this reaction the paramecium swims backward a short distance, stops, and describes a cone by rotating and swerving, until it again moves forward spirally (Fig. 174 D). As the new course may leave the cone at any angle, the animal

usually proceeds in a new direction each time it again moves forward. If this line of progress brings it again in contact with the obstacle, it repeats the reaction of backing off, describing a cone, and again proceeding. Thus, after one or more of these avoiding reactions the paramecium may eventually make its way around the obstacle by what can be called a method of *trial and error*. Such reactions occur when the cell responds by keeping out of a drop of 0.5 per cent salt solution (Fig. 175 B), or, having entered a drop of acid (Fig. 174 B and 175 D), remains trapped therein because it responds negatively whenever it again comes in contact with the surrounding water. The avoiding reaction is the means by which all such responses are effected. This reaction can be modified only within limits; but by performing

it a sufficient number of times, no matter how blindly, a suitable adjustment to existing surroundings can be effected.

The behavior of *Paramecium* consists of locomotion in a spiral, avoiding reactions, and minor responses such as maintaining contact with objects (Fig. 172). By these activities the animal gives evidence of a capacity of irritability comparable with that found in other organisms.

The term *phobotaxis* is now applied collectively to the reactions of protozoans, such as those just described for the paramecium. Specifically, we have *phototaxis*, a reaction to light; *chemotaxis*, a reaction to chemicals; *thermotaxis*, a reaction to heat; and so on. Most reactions of protozoa are of this phobotactic nature. The term *tropism*, often used synonymously with phobotaxis, is more properly restricted to the forced reactions given to certain stimuli by sessile animals and by plants.

In view of these complex responses it is important to note the so-called *neuromotor system* that has been described for the paramecium and certain other ciliates (Fig. 176). Apparently, this system of fibers and centers is a mechanism of coordination within the limits of a single cell. A question that arises in connection with the behavior of the ciliates is whether these unicellular animals can "learn by experience." The case is not proved, but there are some accounts of what is claimed to be learning and seemingly valid reports of "choice" in the acceptance or rejection of particles or organisms in the feeding of ciliates and certain other protozoa. On a "social" level there is the question of whether anything in the behavior of the ciliates can be compared with the community formation seen in many higher animals, as some investigators have claimed.

Feeding and Metabolism. In feeding, the cilia of the paramecium draw a current of water against the oral region, so that particles like smaller protozoans, bacteria, and organic debris

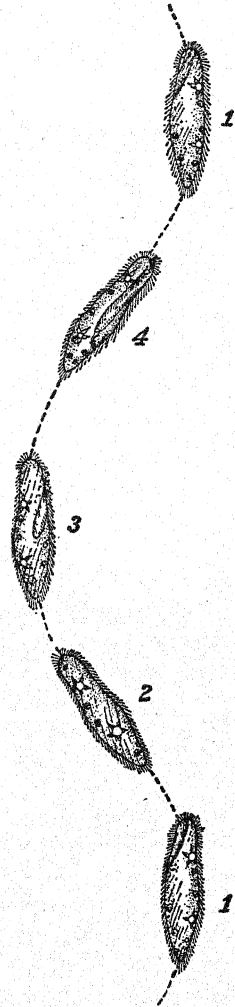


FIG. 173. Spiral path of *Paramecium*. The figures 1-4 show the successive positions assumed in making a complete turn of the spiral.

(From H. S. Jennings, *op. cit.*, reprinted by permission.)

enter the gullet (Fig. 171 Above). By means of the cilia and by movements of the gullet, masses of this food included in a drop of water pass into the protoplasm and are thus *ingested*. The *food vacuoles* so formed move along a definite course within the endoplasm. As in *Amœba*, it is presumed that enzymes are secreted into the vacuoles and bring about *digestion*. The digested food is evidently transferred

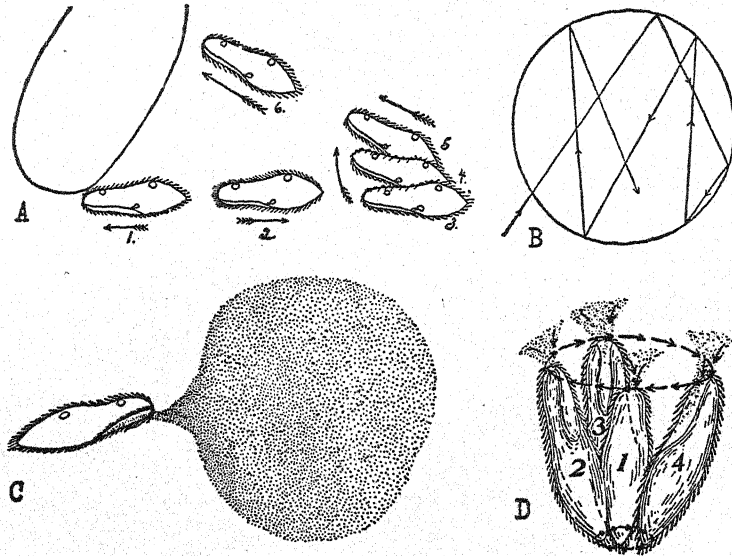


FIG. 174. Reactions of *Paramecium*. A, avoiding reaction; 1-6, successive positions occupied by the animal, not showing the rotation on long axis. B, path followed by an individual trapped in a drop of acid. C, *Paramecium*, near a region containing India ink (shown by the dots); a cone of ink is drawn toward the anterior end and oral groove of the animal. D, *Paramecium*, swinging its anterior end about in a small circle, in a weak avoiding reaction; 1, 2, 3, 4, successive positions occupied.

(From H. S. Jennings, *op. cit.*, reprinted by permission.)

to the surrounding protoplasm, since the vacuole finally contains only material that is *egested* at the anal spot. The observations that can be made upon *Paramecium* are similar to those described for *Amœba*, and one reasons from them in a similar manner with the aid of knowledge concerning other animals. The products of digestion that pass out of the food vacuoles become protoplasm by *assimilation*. *Respiration* corresponds to internal respiration in the frog, since oxygen enters the cell directly from the surrounding fluid. *Dissimilation* occurs by oxidation of protoplasmic constituents, with transformation of energy and forma-

tion of waste products. *Excretion* of the waste products of metabolism may occur by diffusion over the entire surface of the cell or by means of the contractile vacuoles (Fig. 171 Below and cf. p. 248). Under suitable conditions the storage of nutrient materials, such as starches and fats, occurs in the cytoplasm. The nutrition of *Paramecium* is, therefore, holozoic, and its metabolism fundamentally like that of higher animals.

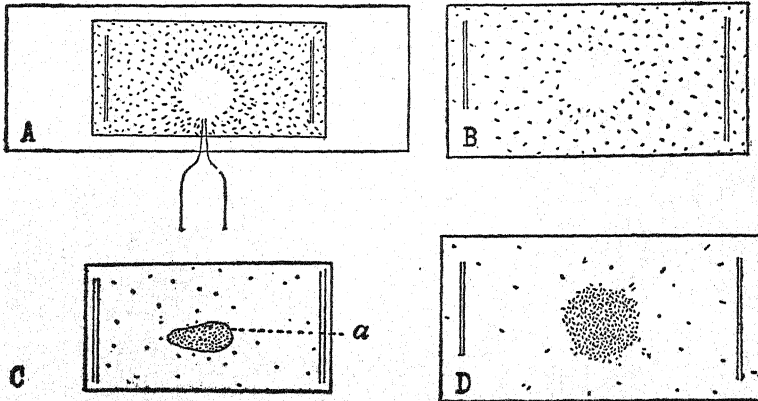


FIG. 175. Reactions of *Paramecium*. A, method of introducing a chemical solution into a slide of ciliates. B, slide of paramecia four minutes after the introduction of a drop of 0.5% salt solution; the drop remains empty. C, a slide of paramecia is heated to 40 or 45° C.; then a drop of cold water (represented by the outline *a*) is placed on the upper surface of the cover-glass; the animals collect beneath this drop, as shown in the figure. D, collection of paramecia in a drop of 0.02% acetic acid.

(From H. S. Jennings, *op. cit.*, reprinted by permission.)

Life-cycle and Reproduction. The life-cycle of *Paramecium* consists of an *active phase*, which may continue indefinitely in a suitable medium. There is no encysted phase that may commonly be observed in the laboratory as in many other ciliates, although encystment has been described. Perhaps it occurs more frequently in nature, since it is difficult to understand how any protozoan can be so universally distributed in fresh water without undergoing occasional encystment as the only means of surviving periods of drought. However, the paramecium does not seem to encyst upon vegetation as do many ciliates, because it is rarely, if ever, obtained by placing such vegetation in sterile water. In the laboratory the life-cycle is an endless active phase with frequent reproduction by transverse *binary fission*, or cell division, and with a periodic nuclear reorganization called

endomixis. Reproduction by *conjugation*, or temporary union of individuals with exchange of nuclear material, may also occur, although some strains of *paramecium* appear capable of maintaining themselves indefinitely, by cell division and *endomixis*, without conjugation.

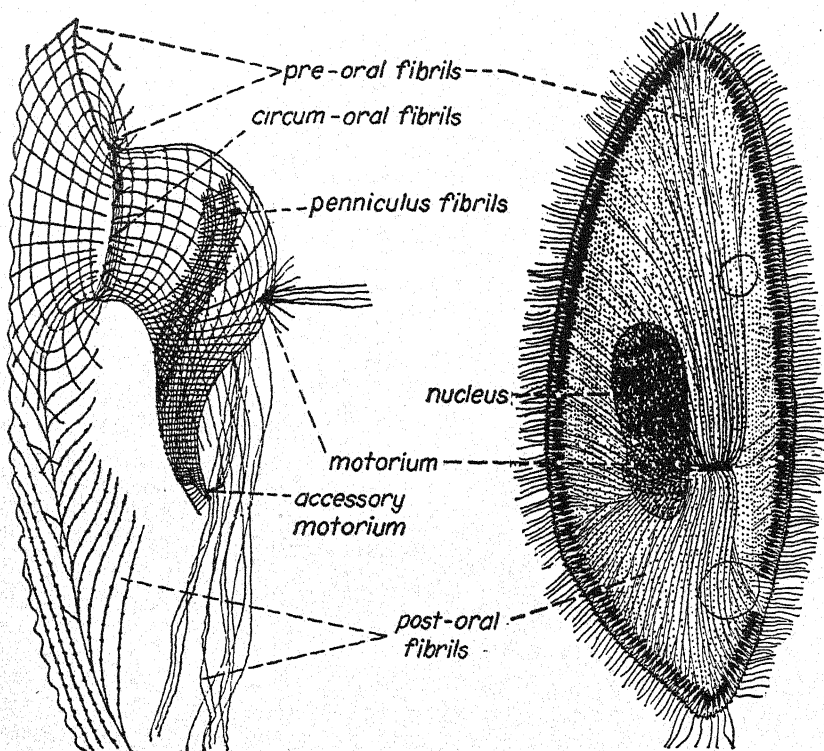


FIG. 176. Mechanism of fibrils and centers in *Paramecium*, called the neuro-motor system. *Left*, the system in region of gullet. *Right*, in aboral view.

(*Left*, from L. H. Hyman, "The invertebrates: Protozoa through Ctenophora," copyright, 1940, by McGraw-Hill Book Co., reprinted by permission. *Right*, after C. W. Rees, University of California Publications, 1922.)

In the binary fission, or cell division, by which reproduction is accomplished, the macronucleus divides amitotically by elongation and constriction (Fig. 177); the micronucleus, by a kind of *mitosis* (cf. p. 107). As division of the two nuclei nears completion, the cell body becomes constricted and finally separates into daughter cells of equal size. Meanwhile, one new contractile vacuole has been formed for each daughter, and new gullets have arisen in each from the oral region of the parent cell. After separation the daughter cells usually

grow to full size before the next division. Under favorable conditions there may be as many as four such divisions, with the production of sixteen individuals, in twenty-four hours. The rate is determined by external conditions, such as food and temperature, and by internal factors.

Although *P. aurelia* and probably other paramecia may live indefinitely without conjugation, this process apparently occurs under natural conditions as well as in the laboratory. In some cultures that

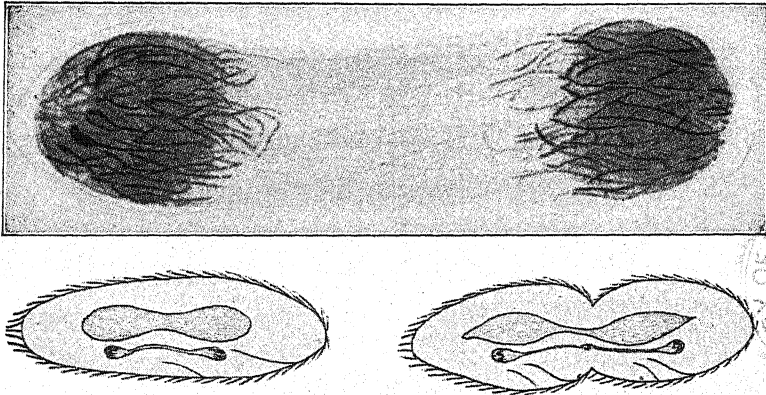


FIG. 177. Asexual reproduction by cell division in *Paramecium caudatum*. Above, division of the micronucleus, showing chromosomes in a polyploid race. Below, binary fission of the cell, showing mitotic division of micronucleus and amitotic division of macronucleus.

(Above, from T. Chen, 1940, *Journal of Heredity*, vol. 31, reprinted by permission.)

were long continued (Calkins, *P. caudatum*), it was observed that conjugation occurred at intervals of some two hundred generations. In others (Woodruff, *P. aurelia*) it was found that conjugation did not occur even in many thousands of generations. The details of conjugation in *P. caudatum*, after the two cells have come in contact in the region of the buccal grooves, are shown in Figure 178, the explanation of which should be consulted. The process differs markedly from the reproduction by permanent fusion of gametes, or syngamy, which occurs in other protozoans. Syngamy results in complete and permanent union of two cell bodies and of their nuclei and resembles the union of the egg and sperm cell during fertilization in higher animals (cf. Fig. 168). Conjugation, which is a temporary union and exchange of nuclear material, as in *Paramecium* and other ciliates, is found nowhere else among Protozoa or other animals. However, the net outcome is the same in syngamy and in

conjugation. In syngamy a single cell is derived with nuclear contributions from two cells. In conjugation two cells unite temporarily,

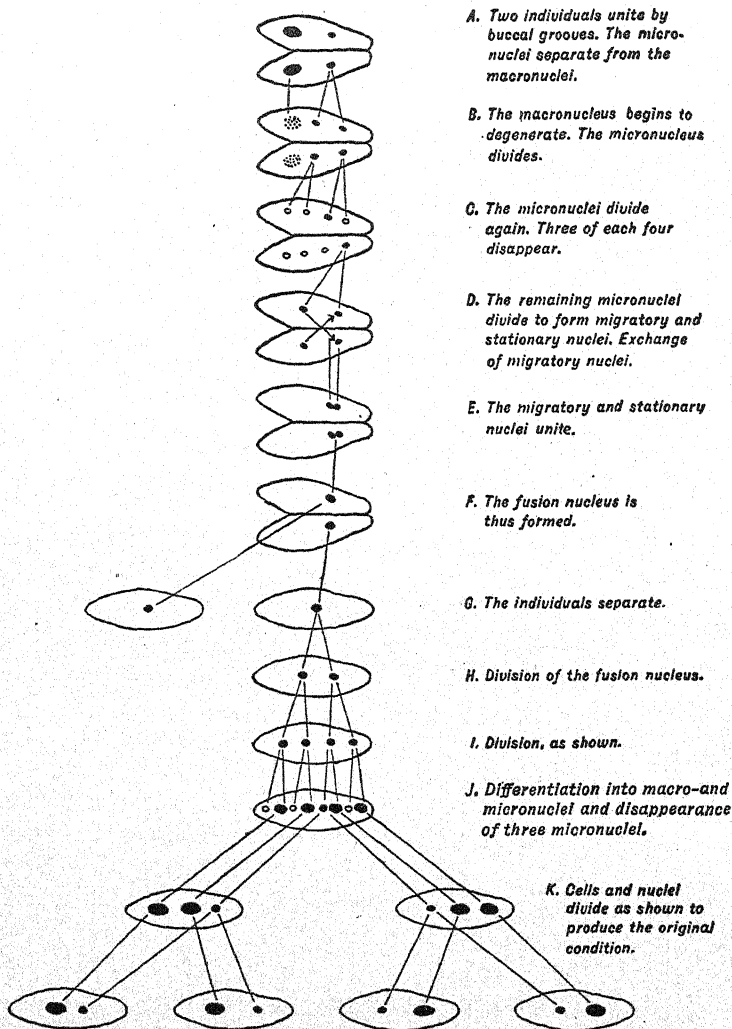


FIG. 178. Conjugation in *Paramecium caudatum*; diagrammatic.

(Redrawn from H. S. Jennings, "Life and death, heredity and evolution in unicellular organisms," copyright, 1920, Richard G. Badger, printed by permission.)

and when they separate each has a nucleus of double origin. Hence, conjugation may be called a special kind of syngamy. Indeed, conjugation is more efficient than the syngamy of fertilization, because the outcome is two cells, the *ex-conjugants*, each with a new combina-

tion of chromosomes; whereas in fertilization the outcome is a single cell, the zygote or fertilized egg. In endomixis the macronucleus and also a considerable portion of the micronuclear material disappear. From a single micronucleus that remains, new macro- and micronuclei are formed. Thus, in endomixis there is a nuclear reorganization comparable with that occurring during conjugation, except that only one cell is involved. Conjugation is called *sexual* reproduction in contrast with the *asexual* reproduction of cell division, although the two members of a conjugating pair are not obviously differentiated as male and female cells.

Within recent years what have been termed *mating types* have been discovered in several species of the Genus *Paramecium*. These mating types fall into groups the members of which will conjugate with one another but not with the members of other groups. The significance of these differences is obscure. Perhaps something akin to sex is involved.

The full significance of conjugation in ciliates is still unsettled. It is clear that the resulting ex-conjugants are individuals with new nuclear combinations and new characteristics, as are the zygotes which result from fertilization in many-celled animals. The question that has led to endless investigation and discussion for more than fifty years is whether conjugation has an important physiological effect upon what may be termed cell vitality, as measured by the rate of cell division, upon the longevity of the race, and upon other normal cell activities. Do these organisms grow old and die unless they are "rejuvenated" by conjugation? In some species such a rejuvenescence seems to occur, but in others no such rejuvenescence has been demonstrated; it does not seem to be universal like the fusion of nuclei, which is the basis for biparental inheritance.

Other Ciliata. Since the Class Ciliata includes most species of large Protozoa that occur commonly in fresh water, it will be reviewed by giving the principal subdivisions and the names of representative genera.

Class Ciliata or Infusoria.

Subclass Protociliata. Cilia of equal length covering entire cell; leaf-shaped or ellipsoidal in shape; no cell mouth; parasitic in intestines of amphibians and fishes. *Opalina* and *Protoöpalina*.

Subclass Euciliata. Cilia and shape of cell specialized as indicated for the several orders; typically free-living but some species in each order parasitic.

Order *Holotrichida*. Cilia of approximately equal length and uniformly distributed over the cell in most species; with or without a cell mouth; without a special oral zone of cilia. *Amphileptus*, *Coleps*, *Colpoda*, *Didinium*, *Dileptus*, *Frontonia*, *Lacrymaria*, *Lionotus*, *Paramecium*, *Prorodon*, etc. (Figs. 179 and 180).

Order *Heterotrichida*. Cilia of cell surface small or reduced in number as compared with the specialized ciliation of oral region. *Nyctotherus*, *Spirostomum*, *Stentor*, etc. (Fig. 179).

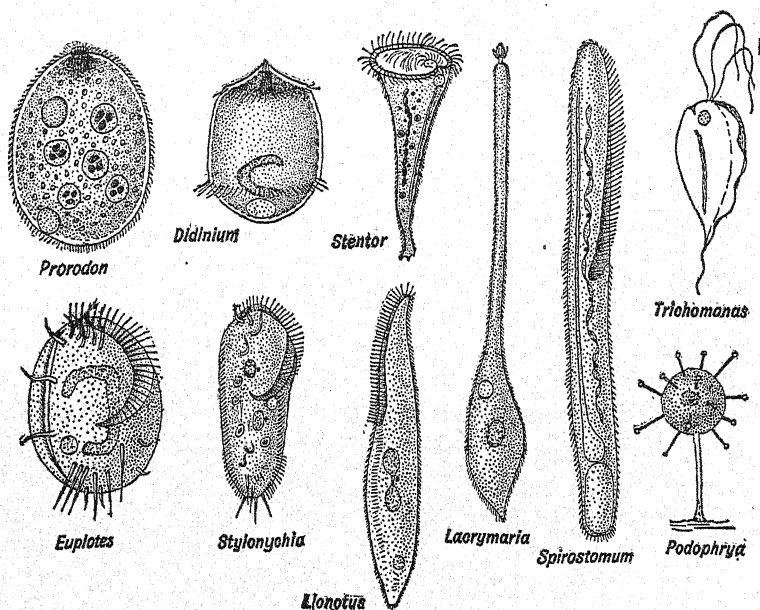


FIG. 179. Common ciliates of fresh water; a parasitic flagellate, *Trichomonas*; and a suctorian, *Podophrya*.

(Drawn in part by Wiley Crawford.)

Order *Oligotrichida*. Cilia greatly reduced in numbers and specialized; mostly parasitic and known principally from the digestive tracts of herbivorous mammals. *Diplodinium*, *Halteria*, *Strombidium*, etc.

Order *Hypotrichida*. Cilia scattered and highly specialized for locomotion and feeding, some as sensory processes; cell usually flattened and with what may be termed dorsal and ventral surfaces; hence, typically creeping forms. *Euplates*, *Oxytricha*, *Stylonychia*, etc. (Fig. 179).

Order *Peritrichida*. Cilia usually restricted to a conspicuous disklike oral region and a basal region at opposite end of cell; the more familiar forms are attached by a contractile stalk. *Carchesium* (Fig. 190 G), *Epistylis*, *Trichodina*, *Vorticella*, *Zoëthamnium*, etc.

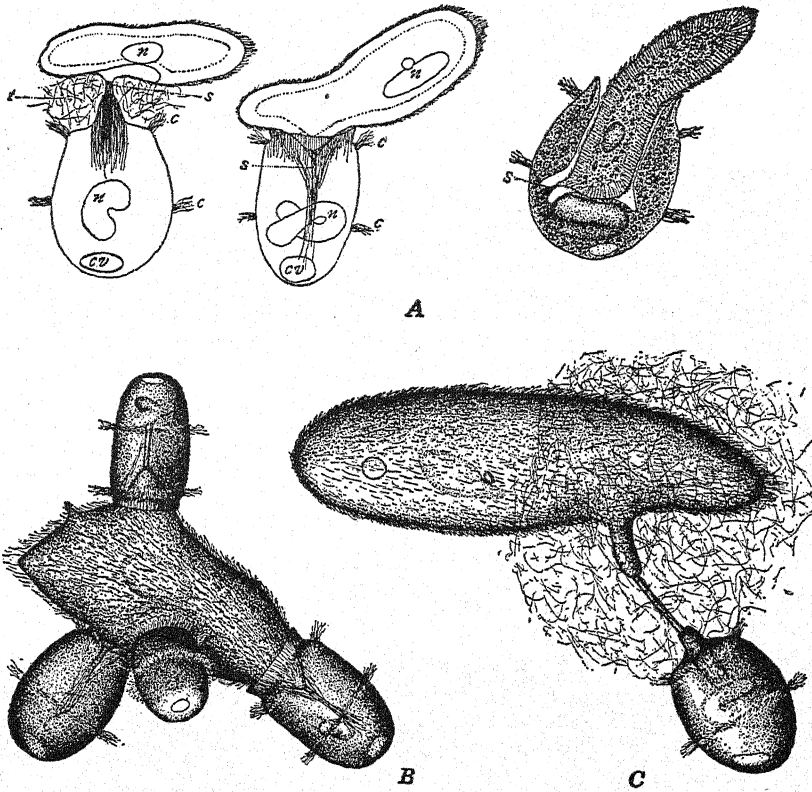


FIG. 180. *Paramecium* attacked by one of its principal enemies, *Didinium nasutum* (cf. Fig. 517, p. 711). A, small *Paramecium* seized by a large *Didinium* and being drawn into the predator, which can engulf such prey completely within a few moments after seizing. B, a large *Paramecium* attacked by four of the predators. C, a large *Paramecium* which has pushed away the predator, apparently by discharge of trichocysts; in such a case the paramecium may escape with a papilla-like deformity of its surface, and the didinium may lose its seizing organ in escaping from the mass of trichocysts.

(From S. O. Mast, 1909, Biological Bulletin, vol. 16.)

The Suctoria

The Class *Suctoria* comprises a small group of Protozoa placed with the Ciliata in the Subphylum Ciliophora, because cilia are present during the motile phase in the life-cycle. During the attached phase of the cycle these cilia are replaced by structures called tentacles, which are used in feeding. The Genus *Podophrya* is a familiar representative and one that is widely distributed in fresh water (Fig.

153 D). The podophrya is attached by a stalk, and its tentacles radiate in all directions from a spherical cell body. Small organisms coming in contact with the knoblike ends of these tentacles are held fast. Apparently the tentacles digest their way through the surface of the captive, since the fluid contents of the prey may be seen later streaming down through the tentacles into the podophrya as the prey slowly shrivels until released as a crumpled mass if it is small enough to be destroyed in this manner. Frequently the podophrya attacks ciliates much larger than itself, such as *Paramecium*, which is sometimes seen swimming with the podophrya attached (cf. Fig. 153 D). When reproduction by cell division occurs, a ciliated daughter cell is detached from the distal surface of the parent and swims until it becomes attached and loses its cilia with the development of a stalk and tentacles. In the ocean several genera of suctorians are common in shallow water attached to various objects so they may be easily collected. The tentacles and shape of the cell are variously modified, but all members of this small group are essentially like the podophrya.

Biogenesis

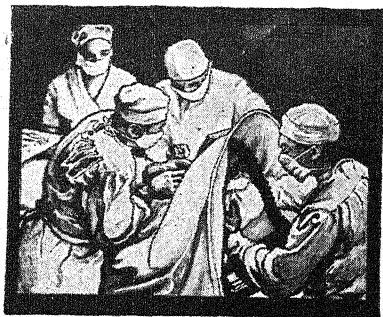
Historical. Some general problems that are intimately related to unicellular organisms may now be examined. One such problem involves the origin of living forms, or *biogenesis*. As a result of investigations extending over more than two hundred years, it was shown during the third quarter of the nineteenth century that *abiogenesis*, or the spontaneous origin of organisms, does not occur. Organisms come from preëxisting organisms by the processes of reproduction. It was natural for the ancients to believe that animals such as insects, which suddenly swarmed in certain places, were produced from the mud of the fields under the influence of the sun's rays or arose spontaneously within the decomposing carcasses in which they were found. It was even supposed that mammals arose spontaneously within the female, although under the influence of seminal fluid from the male.

The higher animals were known to have parents, but the nature of the continuity between generations was not comprehended, save as the eggs of birds and reptiles produced young, and mammals gave birth to living offspring. Gradually it was recognized that smaller animals also arise from eggs. The Italian naturalist, Redi, performed experiments (1688) that showed how maggots originate in meat from eggs laid by flies. He placed meat in jars, covering some with wire gauze and some with parchment, and leaving others uncovered. Flies were attracted and laid their eggs upon the meat or upon the gauze.

Maggots were seen to hatch from these eggs and to grow as they consumed the meat. The pupal stage and the emergence of the adult flies were observed (*cf.* Fig. 381, p. 515). Maggots also hatched from eggs transferred from the gauze to the meat. The meat in the parchment-covered jars decomposed without the appearance of maggots. Redi made other observations upon the development of insects and reached the conclusion that all spontaneous generation was presumably due to the introduction of living "germs" from without.

In 1676 the Hollander, Antony van Leeuwenhoek, discovered with the microscope, which had recently come into use as a scientific instrument, what he described as "little animals observed in rain, well, sea, and snow water as also in water wherein pepper had lain infused." Among other forms of life he observed some of the larger bacteria and many protozoans. During the eighteenth century the observations of Leeuwenhoek were extended by other workers until the important types of microscopic animals became known. Although it was seen that larger organisms arose from eggs or seeds, one could still believe that microorganisms arose spontaneously if conditions were suitable. This belief was not unnatural in view of the sudden appearance of these forms in the great numbers often observed in laboratory cultures. Some biologists from Redi onward, reasoning by analogy with higher organisms, believed that microorganisms arose from preexisting forms. Others clung to belief in spontaneous generation. In spite of repeated failures to find evidence of abiogenesis, the question was reopened on theoretical grounds by Pouchet in 1859.

Final Establishment of Biogenesis. The work of Pasteur (1822–1895) and his contemporaries, about 1860–1864, was stimulated by this final reopening of the problem. A series of brilliant researches by this great Frenchman, by the German, Koch (1843–1910), and by others finally showed that even the smallest organisms arise by division from parent forms (Fig. 182). Species of protozoans and of bacteria were followed stage by stage until the life-cycles of representative types were known in their active and in their resting phases. The English physicist, Tyndall, during investigations upon light about 1876 studied the "floating matter of the air" and showed that it teems with spores and other resistant stages of microorganisms which need only to settle upon a proper medium to germinate (Fig. 185). The English surgeon, Lister (1827–1912), and others who investigated the germ theory of disease as applied to surgery demonstrated that the germs found in wounds are not generated within the body but are introduced, as the spores or the active stages of such minute organisms may be introduced into a sterile culture medium (Fig. 181). The

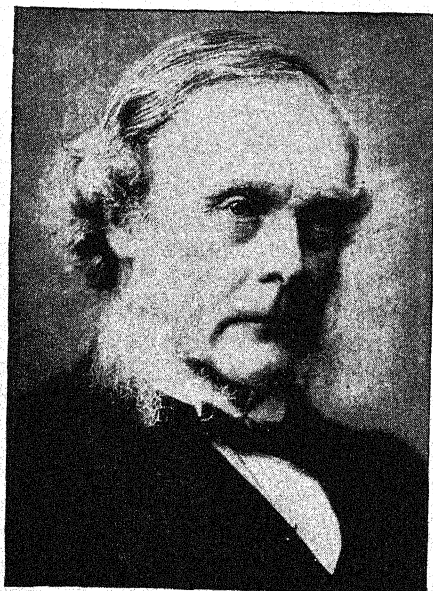


THE SURGICAL "TEAM"



A HOSPITAL BEFORE THE TIME OF LISTER

A PATIENT IN BED WITH A CORPSE. THIS SORT OF THING OCCURRED IN THE CROWDED CHARITY HOSPITALS OF EUROPE TWO CENTURIES AGO



THE STONE AGE OF SURGERY



AN AMPUTATION IN 1793

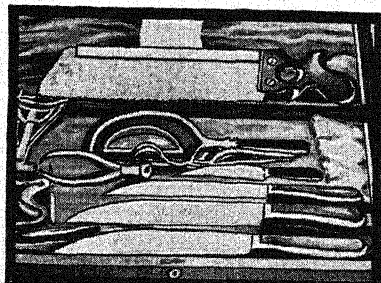
BEFORE THE TIME OF LISTER, PATIENTS ENDURED THE PAIN OF OPERATIONS WITHOUT ANY KIND OF ANESTHESIA.
(FROM A PRINT BY ROWLANDSON)



STAPHYLOCOCCUS
FROM AN ABSCESS
(ENLARGED 1000 DIAMETERS)



STREPTOCOCCI
FROM BLOOD POISONING
(ENLARGED 1000 DIAMETERS)



A SET OF SURGICAL INSTRUMENTS
OF THE EARLY EIGHTEENTH CENTURY

Fig. 181. Sir Joseph Lister and surgery.

(From Biology Briefs, February, 1940; courtesy Denoyer-Geppert Co.)

extension of these demonstrations and of the Cell Theory completed the overthrow of abiogenesis and established biogenesis as the true explanation of the origin of new individuals. Hence, the saying of an earlier time, *omne vivum ex ovo*, every living thing from an egg, and the later one, *omnis cellula e cellula*, every cell from a cell, express the facts as now established.

The long controversy over biogenesis was related throughout to the observation that infectious diseases spread and multiply like

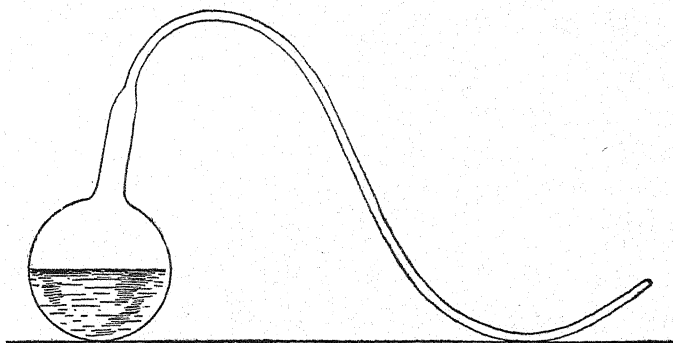


FIG. 182. Pasteur's flask. A sterile solution was placed in the flask, the neck of which was then heated and drawn out into a long tube with a bend in it; no putrefaction developed in the flask because bacteria were unable to get past the bend in the absence of air currents to carry them.

living organisms. When it was discovered that organisms living as parasites are the conditioning factors in such diseases, the basis for the facts observed became apparent. One of the unsolved problems that remained was the increasing number of diseases in which no parasitic organisms could be discovered, although the disease was infectious. In these cases it seemed that "something," which came to be called a *virus*, was present and increased in volume like an organism during growth. A virus was shown to be something invisible, which could pass filters capable of holding back ordinary bacteria, and which was unable to multiply in the absence of the living cells in which it was found, although it could be transferred to other cells and so continue its multiplication (Fig. 183). Among the diseases now known to be caused by viruses are the sleeping sickness called encephalitis, hog cholera, infantile paralysis, parrot fever, small-pox, yellow fever, and a long list in plants, notably the mosaic disease of tobacco. Recently, it has been shown by W. H. Stanley and others that the virus of the tobacco mosaic can be prepared as a crystalline

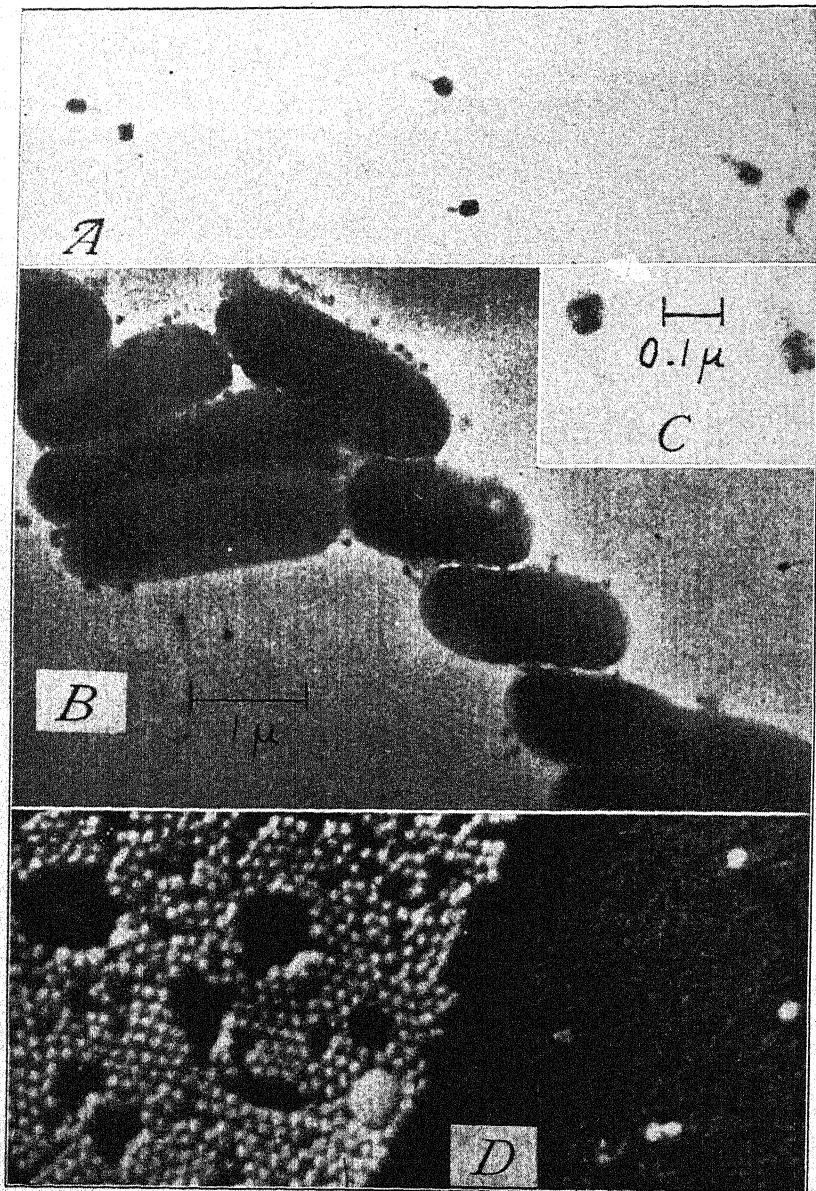


FIG. 183. Bacteriophages and virus molecules as shown by electron microscope. *A*, bacteriophage anti-coli PC, magnified about 29,000 diameters as here printed; note the tail-like appendage. *B*, the bacillus *Escherichia*, in a suspension of bacteriophage anti-coli PC for ten minutes, showing the bacteriophage attacking the bacilli. *C*, bacteriophage anti-coli PC, magnified about 75,000 diameters as here printed. *D*, molecules of the bushy stunt virus, photographed by a special process involving deposit of a thin film of gold upon the object.

(*A*, *B*, and *C*, from S. E. Luria, 1942, Proceedings National Academy of Sciences, vol. 28. *D*, from Williams and Wycoff, 1946, Journal of Applied Physics, vol. 17. Courtesy authors and journals.)

COMPARATIVE SIZES OF VIRUSES

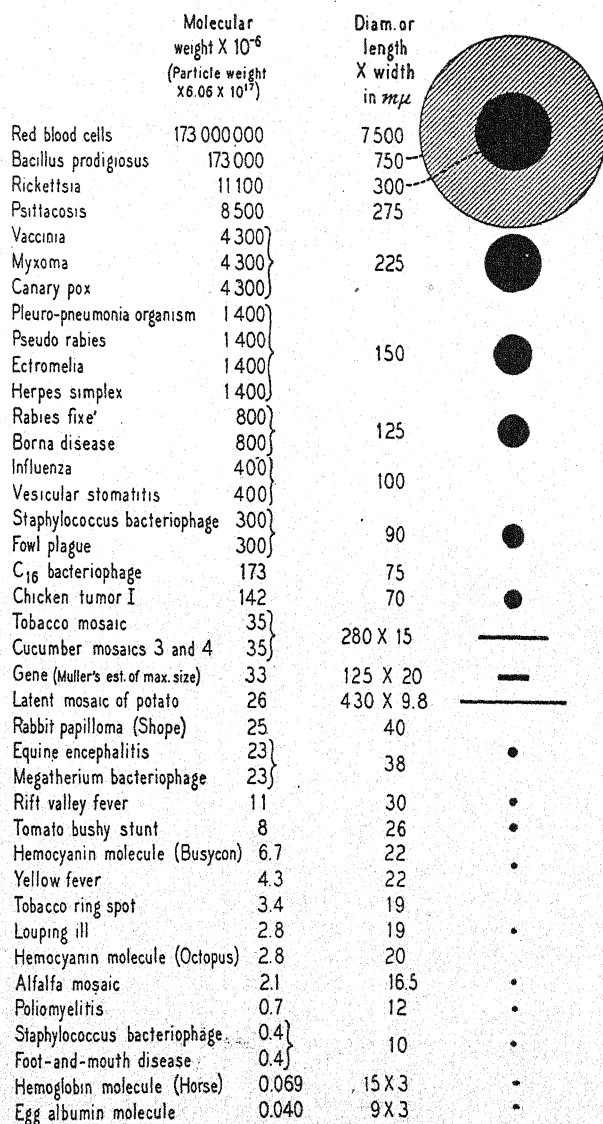


FIG. 184. Sizes of viruses in comparison with a blood cell, a bacillus, and the molecules of the proteins hemoglobin and egg albumin. The figures given are millimicrons.

(From a chart by W. M. Stanley, Rockefeller Institute, Princeton, N. J. Courtesy Dr. Stanley.)

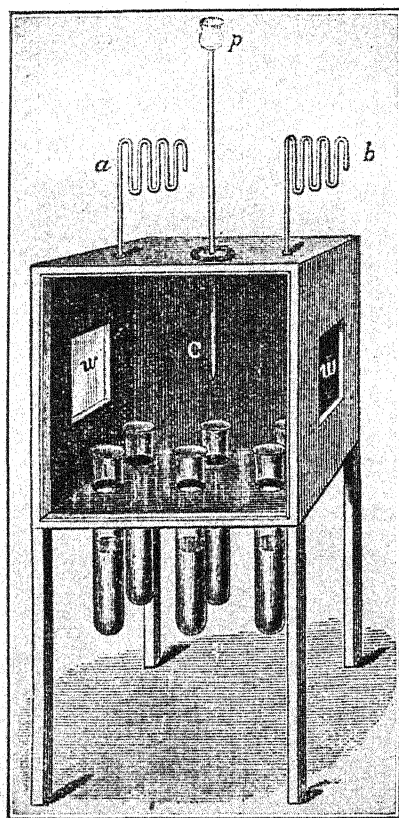


FIG. 185. Tyndall's chamber. The chamber consisted of a box with a glass front and windows (*w*) and with test-tubes fitted tightly in the bottom. Air could enter the chamber by the tubes *a* and *b*, but the entrance of particles floating in the air, such as dust and bacterial spores, was prevented by bending these tubes. A pipette (*c*) that entered the chamber through a rubber diaphragm could be moved to place material in the different test-tubes. This pipette was plugged with cotton at *p* when not in use.

In the experiments, the chamber was tightly sealed and left undisturbed for a few days until the particles floating in the air had settled to the bottom, as indicated by the fact that an intense beam of light, when passed through the windows, failed to show its track within the chamber. Various nutrient fluids, such as hay infusion, beef broth, etc., were then introduced into the test-tubes and boiled for five minutes. Although the chamber was placed in a warm room, there was not a single unexplained case in which such an infusion showed any signs of life. That the observed sterility was not due to any lack of nutritive power in the infusions was proved by opening the door of the chamber and permitting entrance of the external air with its suspended particles.

(From J. Tyndall, "Floating matter of the air," copyright, 1888, by D. Appleton and Co., reprinted by permission.)

molecule which is infective in the same manner as the virus in nature. According to Dr. Stanley, infection with a virus disease may be regarded as the introduction of a few molecules of a virus protein into the living cells of a suitable host. These few molecules produce more of their kind at the expense of the host's metabolism, and so the host is profoundly affected. The disease may be regarded as a disruption of the normal metabolism in the host cell. In size (Fig. 184) the viruses range downward from giant molecules, nearly visible with the microscope, to the size of many other molecules not known to possess the capacity of reduplication that characterizes a virus. Whatever the conclusion, the further study of viruses is likely to yield results of importance not only in the control of many diseases but also for our understanding of the nature of protoplasm.

Protozoa and Disease

What is known as the Germ Theory of Disease postulates that certain diseases are conditioned by specific germs, or minute organisms that live as parasites in the bodies of plants or animals. The symptoms of the disease are the reactions of the host in response to such parasitic invasions. In general, the so-called *infectious diseases* are correlated with organisms which infect the body and whose normal existence is parasitic in this phase of their life-cycles.

Malaria and the Malaria Parasite. The disease called malaria has been known since ancient times. Some investigators have even regarded it as largely responsible for the decline of ancient Rome. Certain it is that both Romans and Greeks, and probably other ancient peoples, suffered greatly from this pestilence. Early explorers of the Americas found it established in the tropical regions of both continents and brought back to Europe the South American Indian's medicine, "Peruvian bark" of the cinchona tree, from which quinine was later extracted. At present the seriousness of the disease in all the warmer parts of the world is a problem for statesmanship as well as for medicine.

The word malaria, which means "bad air," was originally applied to a group of fevers associated with swampy regions. The idea that the air of such a region acts as the causative agent is still prevalent among the ignorant; but, if there are no mosquitoes to act as intermediate hosts for the parasite, there is no malaria. The germs in this instance are Sporozoa, such as *Plasmodium malarix*, which is the parasite in one type of the disease. In man the parasite lives in the blood, invading the red cells where reproduction occurs by a kind

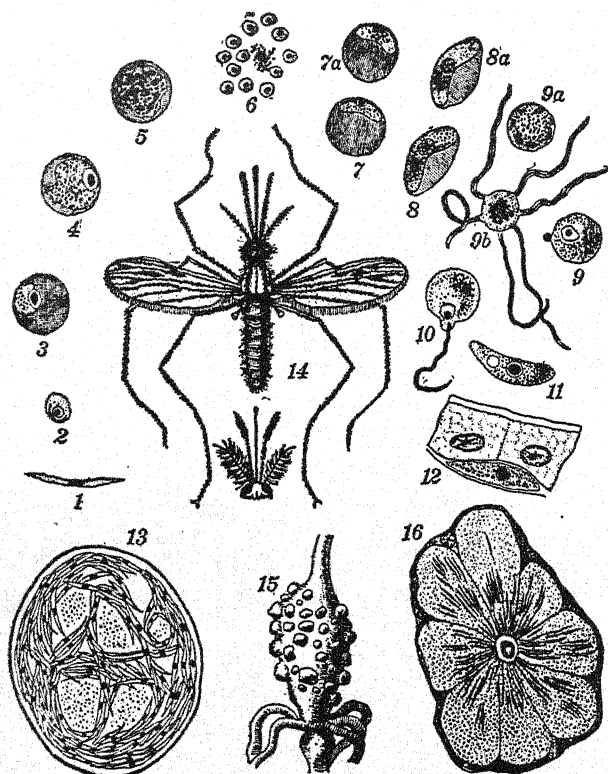


FIG. 186. Life-cycle of the parasitic protozoan, *Plasmodium malariae*, which is the cause of quartan malaria in man. 1, the parasite, known as the sporozoite, as it is introduced into the blood of man by the bite of a mosquito; 2, 3, 4, and 5, sporozoite entering red blood cell where it grows and reproduces new individuals by sporulation; 6, destruction of blood cell resulting in the liberation of these new individuals, known as merozoites, and of excretory or melanin granules into blood plasma; 7, 7a, 8, and 8a, formation of male and female gametocytes in red blood cell; 9, formation of a macrogamete in the stomach of a mosquito; 9a and 9b, formation of microgametes in the stomach of a mosquito; 10 and 11, union of a macrogamete with a microgamete to form a zygote in the stomach of a mosquito; 12, zygote after penetrating the epithelium of a mosquito's stomach; 13, sporozoites formed by divisions of the zygote within its cyst; 14, female mosquito that transmits malarial parasite, with the head of a male below; 15, external surface of a mosquito's stomach, showing swellings produced by encysted stages formed by division of zygotes, as shown in 13; 16, section of salivary gland of a mosquito, showing sporozoites that have been freed from cyst and have migrated through the body cavity to the gland cells, where they lie ready to be discharged into the blood stream of man when the mosquito feeds.

(After the Leuckart-Chun chart, from T. Hough and W. T. Sedgwick, "Human mechanism," copyright, 1918, by Ginn and Co., reprinted by permission.)

of multiple cell division known as *sporulation*, in which there are repeated nuclear divisions before the cytosome divides (Fig. 186). The new parasites are liberated with destruction of the red cells and in turn invade new cells, in which the process is repeated. In this manner a very large number of these blood cells may be destroyed, and the numbers of the parasites greatly increased. Waste products, in the form of melanin granules and probably also poisons, called toxins, that may be set free in the blood stream with the liberation of the parasites from the disintegrating cells, appear to be the specific substances that induce the chills and fever, since this liberation and the ague of the patient both occur at intervals of about seventy-two hours. After a considerable period of such multiplication, the parasite forms *macrogametocytes* and *microgametocytes* which remain in the blood cells of man until blood is sucked by a mosquito. In the stomach of the new host, the gametocytes differentiate into *macrogametes* and *microgametes*, and *syngamy* occurs. The resulting *zygote* passes through the epithelium of the mosquito's stomach wall and takes up a position as shown in Figure 186. Reproduction by *sporulation* again occurs as a result of repeated cell divisions, and eventually many spindle-shaped cells, the *sporozoites*, are formed. The cyst formed about the mass by the host's tissue finally bursts, and the cells thus liberated migrate through the body spaces to the salivary glands, from which they are ejected with saliva when the mosquito bites a human being. And so the cycle begins again.

Quinine was used for the treatment of malaria long before anything was known regarding the parasites that cause the disease. Scarcity of quinine created an acute problem for the South during the American Civil War, as well as for us and our allies during World War II. As a result of the recent scarcity an intensive program of research was instituted in the search for drugs with antimalarial properties. The outcome has been a better definition of the problems involved and greater success in the suppression and cure of malaria. It has been found that the drug quinaquine (atabrine) is superior to quinine when properly used, and compounds superior to quinaquine have been discovered, notably several members of the aminoquinoline series. Eventually, the research in this field should yield the information needed for a more effective control of malaria than has been possible in the past.

Life-cycles in which there are similar primary and intermediate hosts are not uncommon among parasites (*cf.* p. 365). The present example also illustrates the relationship of insects to disease-producing organisms. The following are representative cases affecting man:

yellow fever, transmitted by mosquitoes but not by the same genera that transmit malaria; typhus fever and trench fever, transmitted by the body louse; Rocky Mountain spotted fever, by a wood tick; Japanese flood fever, by a mite; elephantiasis, in which the parasite is one of the roundworms, transmitted by mosquitoes (*cf.* Fig. 280 B, p. 392); relapsing fever in man and Texas fever in cattle, by ticks; and bubonic plague, by fleas.

Dysentery and *Endamoeba histolytica*. Most of the amœbas are free-living, like the species commonly seen in the laboratory. A

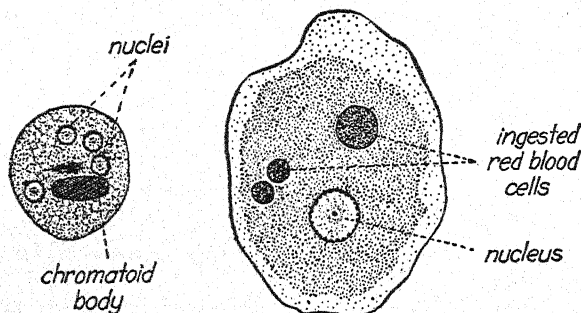


FIG. 187. The intestinal amœba, *Endamoeba histolytica*. Left, a cyst with the four nuclei characteristic of this stage. Right, the active stage. Both from stained specimens, magnified about 1250 diameters as here printed.

(Modified from A. C. Chandler, "Introduction to parasitology," John Wiley and Sons, copyright, 1944, by author, printed by permission.)

smaller number of the known species are parasitic, and one of these, *Endamoeba histolytica* (Fig. 187), causes the serious disease of man called *amœbic dysentery*. This amœba is found in the large intestine of man and sometimes in the lower part of the small intestine as well. In advanced cases the parasites may be carried by the blood to the liver, lungs, and brain, where they cause serious abscesses; indeed, almost any part of the body may be thus invaded in exceptional instances. Most commonly, the parasite is restricted to the large intestine, where it destroys the mucous membrane (*cf.* Fig. 57, p. 105), thus coming in contact with the submucosa, which is richly supplied with blood vessels. The ulcers of the intestine so formed become infected with bacteria, as well as with *E. histolytica*. The food of the parasite consists of the tissues it destroys and more specifically of red blood cells. Hence, the symptoms of the disease are not confined to intestinal disturbances.

The *active stage* of the parasite may be observed in the freshly discharged feces of the host, moving in amœboid fashion by advanc-

ing one side of the cell as a single broad pseudopodium (Fig. 187 A). The ectoplasm is clear; the endoplasm is finely granular, containing many ingested red blood cells in food vacuoles and the single nucleus. The active stage becomes sluggish as the feces cool and dies within a few hours. The *encysted stages*, which are also discharged in large numbers in the feces, are smaller cells encased in globular cysts and having typically four nuclei (Fig. 187 B). They can survive for some time outside the host and are moderately resistant to heat and cold, although they can be killed by the pasteurization of milk and by the heating of water. The only practicable methods of destroying them in drinking water are boiling or suitable filtration. These cysts are transferred to the intestine of a new host via the mouth and digestive tract by food and drink and to a lesser extent by other means. Reproduction occurs by *binary fission* in the active stage; and the two nuclear divisions, which produce the four nuclei of the encysted stage, are the forerunners of two cytoplasmic divisions, by which four small mononucleate cells are produced from each multinucleate encysted individual after its *excystment*. These small mononucleate individuals grow into the large active stage.

Once regarded as a tropical disease, amœbic dysentery is now known to be distributed throughout the world, even to the arctic circle. Infections are of common occurrence among underprivileged groups in the United States, and epidemics, such as the one in Chicago some years ago, have occurred. With increasing travel to and from parts of the world where this type of dysentery is common, the disease may cause the people of the United States increasing concern. Fortunately, methods of prevention are well known, although curative treatment is still a problem.

Pyorrhea and *Endamœba gingivalis*. Pyorrhea is a disease of the gums which results in gum recession and eventual loss of the teeth. Laymen as well as dentists are aware that this disease is alarmingly common in the United States and presumably in other countries. *Endamœba gingivalis* (Fig. 188) has been found so frequently in the lesions associated with pyorrhea that it has been regarded as the causal organism, although there is still some doubt whether this amœba is the primary cause or merely an organism that flourishes within the gum lesions after they have been initiated by some other factor. In any case *E. gingivalis* has been found in the mouths of 75 per cent or more of the individuals over 40 years of age in samples of the American population, and it is almost always present in both incipient and advanced pyorrhea. It is certainly true that *E. gingi-*

valis is a parasite in the human mouth, and similar forms have been found associated with pyorrhea in horses, dogs, and monkeys.

The *active stage* of this amœba moves by means of a single broad pseudopodium extended from the side of the cell which is advancing. Since no encysted stage has been found, it would seem that the infection is spread by direct or indirect contacts. The resistance of the active phase, when removed from the mouth, to drying and to higher and lower temperatures bears out such a theory.

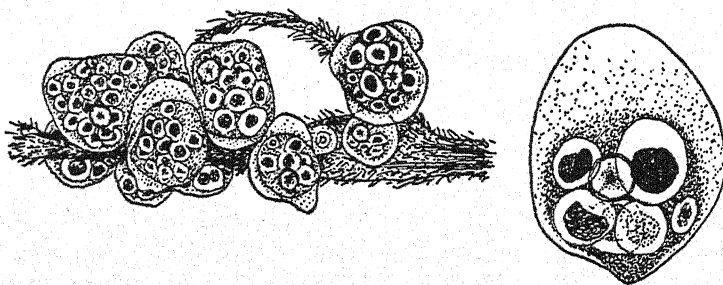


FIG. 188. The mouth amœba, *Endamœba gingivalis*. Left, a cluster of these amœbas on a filamentous mass of *Leptothrix*, a bacillus found in the mouth; each amœba has many food vacuoles containing remnants of the nuclei of white blood cells.

(Modified from A. C. Chandler, *op. cit.*, printed by permission.)

A variety of other amœbas is known to inhabit the intestines of man and other animals, probably many more species than can now be recognized. Most of these appear to be relatively harmless "mess-mates" living as parasites within the larger animal but not markedly disadvantageous to their host.

African Sleeping Sickness and Trypanosomes. Another example of an insect-borne disease is "sleeping sickness," occurring in equatorial Africa and always associated with one of the flagellate protozoans called trypanosomes (Fig. 189). By the bite of the blood-sucking tsetse fly, the stages of the parasites found in human blood are transferred to the intestine of this insect, which serves as an intermediate host. Here a series of stages occur, until some 3 to 4 weeks later the parasites appear in the salivary glands of the fly, from which they may again be transferred to the blood of man or some other mammal. In the final stages of the cycle they invade the cerebrospinal fluid, inducing the sleep that characterizes the disease and finally ends in death. Although these trypanosomes produce a fatal disease in human beings, they produce no obvious effects when they

parasitize some of the larger African mammals. Such a contrast in susceptibility can perhaps be explained on the theory that the mam-

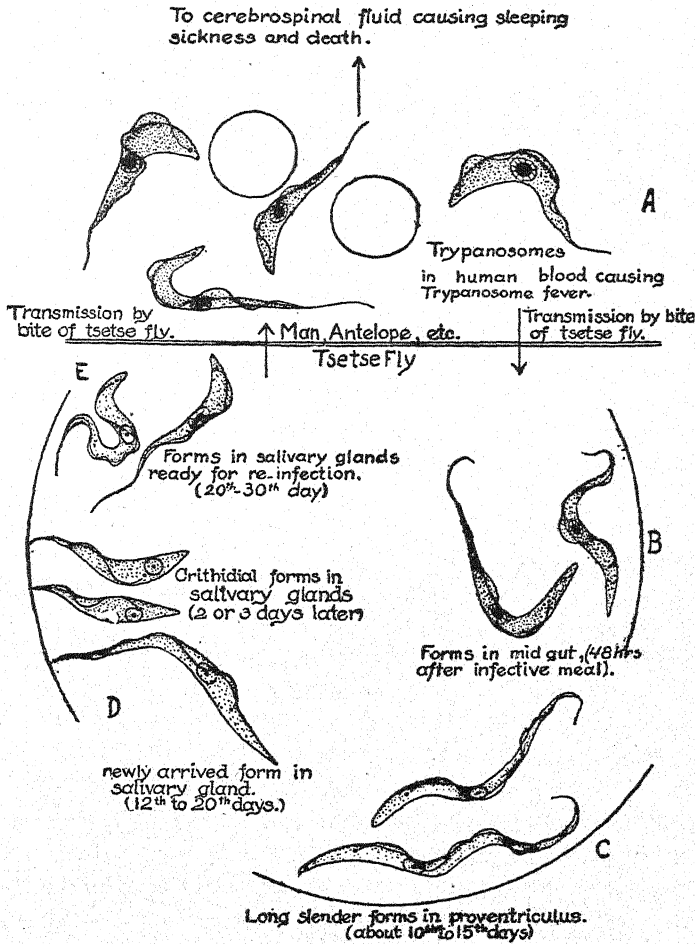


FIG. 189. Life-cycle of the parasite of African sleeping sickness, *Trypanosoma gambiense*.

(From A. C. Chandler, "Animal parasites and human disease," John Wiley & Sons, copyright, 1922, reprinted by permission.)

mals in question have become tolerant of the infection as a result of natural selection, acting upon many generations, whereas man has but recently come in contact with these parasites.

Colonial Protozoa

Although the typical protozoan is a single cell, there are species of Protozoa in which many similar cells live together in groups, called *colonies*, during a considerable part of the life-cycle. The difference between these colonial protozoans and a metazoan lies in the relationship of the individual cell to the other cells with which it is associated. In the adult metazoan the cells can be classified as *somatic cells* and *germ cells*, respectively, depending upon their relation to reproduction (cf. p. 113). This classification is not hard and fast; but in general the somatic cells are specialized for the various functions of metabolism and irritability, whereas the germ cells are specialized for *sexual reproduction*. During the *asexual reproduction* of the metazoan, there may be formative cells (cf. p. 356), which can be called reproductive in so far as they become an important source for cells of the new parts; and for the time being, no cells which are comparable to the germ cells with their strictly reproductive functions may be present. Most important in the metazoan is the fact that the various kinds of somatic cells, as well as the germ cells, are dependent upon the collective activities of the metazoan individual. The cell of the metazoan is a unit subordinated to the activities of the multicellular whole, which is the metazoan.

By contrast, the protozoan cell is an independent, self-sustaining individual. In most colonial protozoans, each cell of the colony is likewise an independent individual, so far as the fundamental capacities of metabolism, irritability, and also reproduction are concerned. In such a species the colony eventually disintegrates by separation of its units so that each cell goes its way, encysting, dividing, conjugating, or uniting with another cell in syngamy, until a new colony is formed again from the single cell by repeated divisions and by the remaining together of the daughter cells. Every cell of the colony is, therefore, as independent functionally as though there were no colonial stage in the life-cycle. Such species are manifestly no more than colonies of independent protozoan cells, each of which is sufficient unto itself, that is to say, is physiologically balanced.

However, in a few species of colonial Protozoa the distinction can be made between somatic cells, which are destined to die, and germ cells, which can continue to live if they become gametes and unite in syngamy. A comparison of these species with the Protozoa, on the one hand, and with the Metazoa, on the other, enables one to align the basic processes of reproduction from one end of the Animal Kingdom

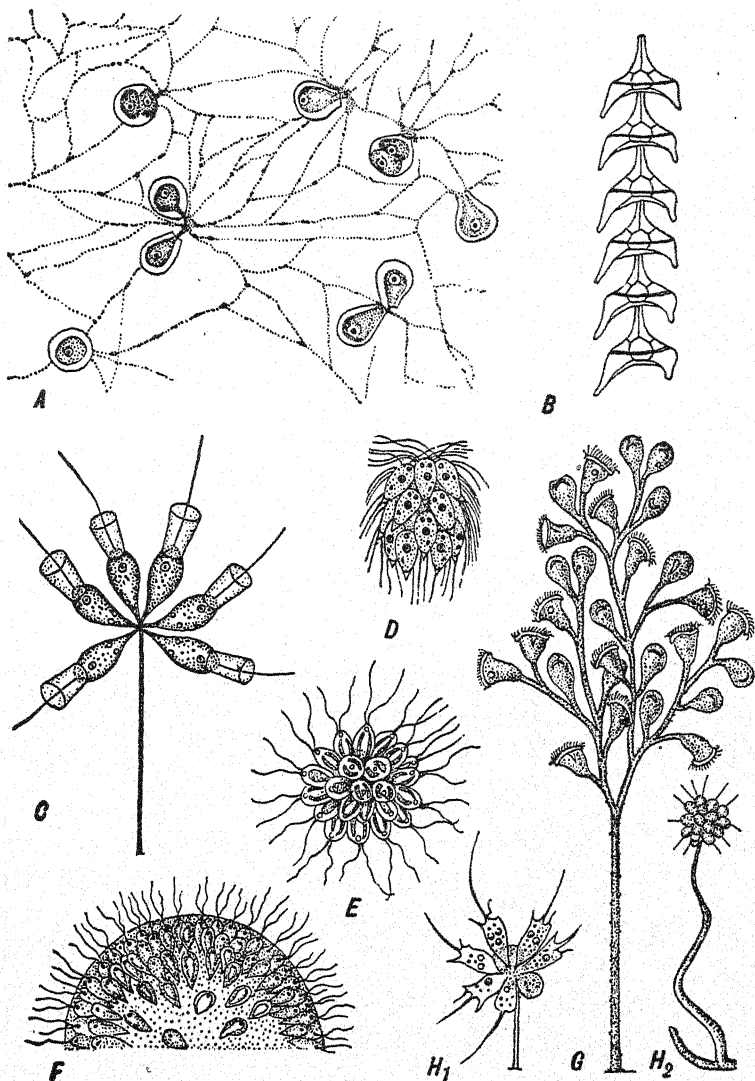


FIG. 190. Types of colonial Protozoa. A, *Microgromia*, a gregaloid colony. B, *Ceratium*, a linear colony. C, *Codonosiga*, an arboroid colony. D, *Spondylomorum*, a spheroid colony. E, *Synura*. F, *Uroglena*. G, *Carchesium*. H₁ and H₂, portions of *Anthophysa* colony.

(Figures redrawn as follows: A, from G. N. Calkins, "Protozoa," copyright, 1901, by The Macmillan Co., printed by permission; C, from E. A. Minchin, "Introduction to study of protozoa," copyright, 1912, by E. Arnold and Co., printed by permission; D, E, F, H₁, and H₂, from F. Blochmann, 1895, "Die mikroskopische Thierwelt des Süsswassers"; G, from W. S. Kent, "A manual of the infusoria," vol. 3.)

to the other, and also, to apprehend facts which justify the belief that the primeval ancestors of both Protozoa and Metazoa were single-celled organisms. To understand this fascinating comparison, one needs, as elsewhere in science, to take a series of isolated facts and to put them together into a rational system, which then becomes an hypothesis to be tested experimentally. Or, if experimental test is impossible, the hypothesis can be tested by a critical reëxamination and by further observations, after which it may become accepted as

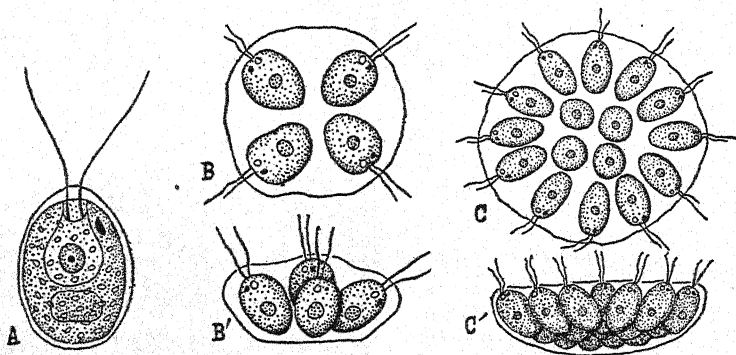


FIG. 191. *Chlamydomonas*, a non-colonial flagellate, and two simple colonial types. A, *Chlamydomonas*. B and B', two views of *Gonium sociale*, a colony with four cells. C and C', two views of *Gonium pectorale*, a colony with sixteen cells.

the most reasonable explanation of the facts that can be offered with the information obtainable. In the remainder of this chapter such a review of facts and relationships is undertaken with respect to the reproductive processes of animals and also the evolution of many-celled from single-celled organisms.

Protozoan colonies are called *gregaloid* if their cells are arranged irregularly; *linear*, if in a line; *arboroid*, if branching; and *spheroid*, if spherical or globular (Fig. 190). Descriptions of some representative spheroid colonies will serve as a basis for further comparisons between colonial Protozoa and Metazoa. A series of forms in the Family *Volvocidæ* will be used, although this family belongs among the Phytomastigina or the mastigophorans that resemble plants rather than animals.

In the Genus *Chlamydomonas*, which is non-colonial, the organism is an oval cell with two flagella, a red pigment spot, a prominent chromatophore containing chlorophyll, two contractile vacuoles, and a cell wall like that in many unicellular plants (Fig. 191 A). Repro-

duction is by binary fission, with immediate separation of the individuals thus formed. Reproduction also occurs by the permanent union of isogametes.

Gonium sociale is a colony of four cells arranged in a single layer and embedded in a gelatinous plate (Fig. 191 B). Each cell has two flagella, a pigment spot, chlorophyll, and a contractile vacuole. Aside from the fact that the colony is propelled as a unit by the flagella, the cells are independent in their functions and hence physiologically

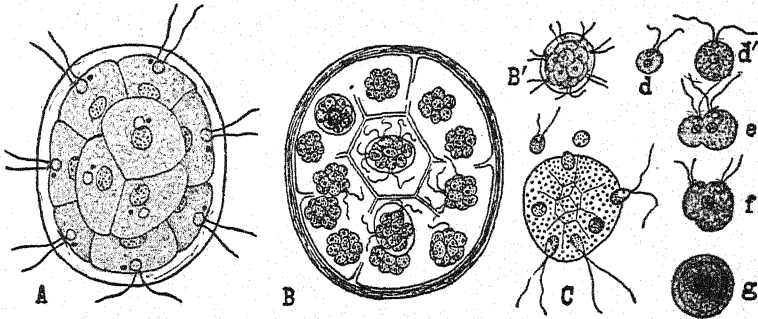


FIG. 192. *Pandorina morum*, a colonial flagellate. A, fully developed colony composed of sixteen flagellated cells. B, formation of daughter colonies by division of each cell to form sixteen. B', daughter colony free of parent colony. C, formation of gametes. d-g, union of microgamete (d) with macrogamete (d') to form zygote (g).

(From F. Oltmanns, 1904, "Morphologie und Biologie der Algen," vol. 1.)

balanced like the cells of non-colonial Protozoa. Reproduction occurs by division of each of the cells to form four daughter colonies, which then separate and grow to the size of the parent colony. Reproduction also occurs when the individuals of the colony separate as isogametes and unite to form zygotes, from which new colonies arise by cell division without separation of daughter cells. In the related species, *Gonium pectorale* (Fig. 191 C), there are sixteen cells in the colony, but otherwise the structure and life-cycle resemble those of *G. sociale*.

Pandorina morum consists of eight or sixteen cells, rarely thirty-two, fitted together in an oval mass and surrounded by a common gelatinous envelope (Fig. 192). Each cell has two flagella, a pigment spot, chlorophyll, and a contractile vacuole. As in *Gonium*, the flagella beat so that the colony swims as a unit, although in other respects its cells are physiologically independent. In reproduction each cell may divide to form miniature colonies of sixteen cells, which break

through the envelope of the parent colony and grow to full-sized colonies before repeating the process; or the cells of the colony may separate as isogametes, which unite to form zygotes from which new colonies arise. Anisogametes have been described in some instances. If these accounts are correct, *Pandorina* is a form showing a transition from isogamy to anisogamy.

Eudorina elegans is a colony of eight, sixteen, thirty-two, or even sixty-four flagellate cells resembling those of *Pandorina*. In reproduction, daughter colonies are formed by division of each cell, as in *Pandorina*, and by anisogametes which unite to form zygotes, from which new colonies arise by cell division (cf. Type 4, Fig. 194). In *Eudorina* the macrogametes and microgametes arise in different colonies.

Pleodorina illinoisensis is a group of thirty-two flagellate cells, of which twenty-eight are larger and capable of reproduction by cell division as well as by forming anisogametes, whereas the four remaining cells are smaller and incapable of reproduction. These four cells may be regarded as somatic cells. In another species, *P. californica*, there are either sixty-four or one hundred and twenty-eight cells. Of these cells approximately one-half are somatic cells, which are physiologically unbalanced since they cannot form gametes and must eventually die. The remaining cells may be called germ cells, because they can form gametes.

Volvox globator is representative of the Genus *Volvox*. The individual, or colony, is composed of several thousand cells arranged at the surface of a sphere, the interior of which is filled with a watery fluid (Fig. 193). Each of these cells consists of a mass of cytoplasm surrounding the nucleus and connected with the cytoplasm of neighboring cells by radiating strands which perforate the cell walls. Each cell has two flagella, a red pigment spot, a contractile vacuole, and chlorophyl. Germ cells appear when some of the cells enlarge and protrude into the central cavity, retaining their connection with the surface. Some of these germ cells grow into the macrogametes, or ova, which retain their position within the parent colony. Others divide repeatedly to form groups of microgametes, or spermatozoa, which are discharged into the water upon reaching maturity. When the mature spermatozoön has been discharged and is moving about in the water, it may come in contact with an ovum and fertilize it. The zygote thus formed secretes a cyst about itself and after a quiescent period emerges from this cyst and produces a new colony by cell division. In the meantime the parent colony has disintegrated with the death of its component somatic cells. Some species of *Volvox* also reproduce by forming cells called *parthenogonidia*, which resemble

macrogametes but are capable of dividing to form new colonies in the same way that all the cells of *Pandorina* can give rise to new colonies. The great majority of the cells of *Volvox*, which do not become gametes or parthenogonidia, are somatic cells and eventually die, like the cells composing the bodies of multicellular animals. In *Volvox* all the somatic cells are similar; that is, no specialization of somatic cells occurs. In a complex animal, such as a vertebrate, there are many

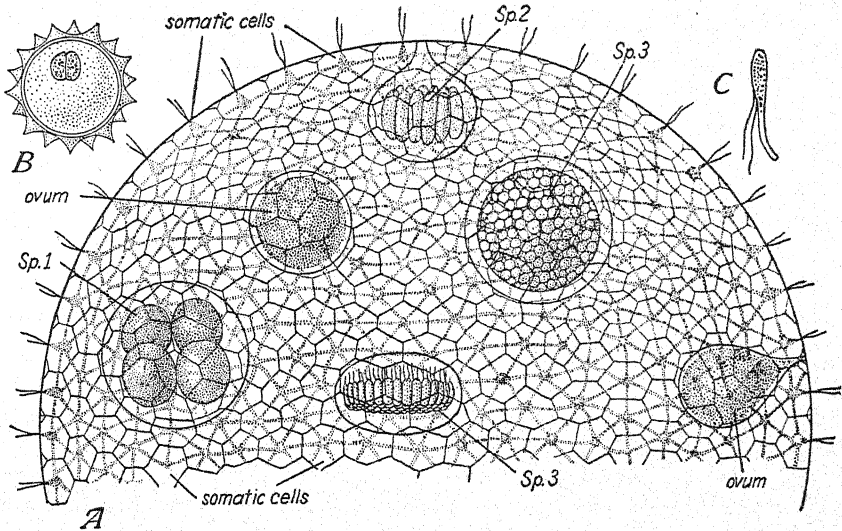


FIG. 193. *Volvox globator*, a colonial flagellate. A, one-half of the spherical colony. B, zygote, with male and female nuclei uniting, and protective shell secreted after fertilization. C, microgamete or spermatozoön. Sp. 1, 2, and 3, developing sperm-spheres.

kinds of somatic cells which have become specialized in the course of the development from zygote to adult (Fig. 90, p. 149). Since the occurrence of somatic cells indicates the loss of physiological balance which is characteristic of the cells of Metazoa, it is possible to regard *Pleodorina* and *Volvox* as multicellular organisms rather than colonies of protozoan cells (cf. Type 5, Fig. 194).

The protozoan life-cycles described in the preceding paragraphs and in earlier sections of this chapter may now be reduced to the generalized diagrams shown in Figure 194. In this way we can compare these cycles with those of higher animals.

In the species represented by *Type 1* the cycle consists, so far as is now known, of an endless series of cell divisions, since neither syngamy nor conjugation has been described. The only reproduction in such

a cycle is the asexual reproduction by cell division. Encystment may occur in Type 1 and others of the series but is disregarded throughout the figure, because it is not important for the present comparisons.

Type 2 represents the cycle of species which exhibit, in addition to cell division as in Type 1, a fusion of similar cells, in other words, an isogamous syngamy. By showing one of the original individuals with a black nucleus and a black-white combination after syngamy, the biparental combination resulting from the syngamy is indicated. This type, therefore, exhibits the asexual reproduction of cell division and the sexual reproduction of syngamy.

Type 3 represents the cycle in most Ciliata. There is cell division comparable with that of Types 1 and 2 and in addition the unique type of syngamy that occurs in these protozoans, whereby two individuals unite temporarily and exchange nuclear material. The outcome in each ex-conjugant is a biparental combination as in Type 2, although the mode of syngamic union is not the same. For the purpose of Figure 194 this Type 3 might be omitted. For the sake of completeness it is included to show how conjugation differs from the syngamy of all other Protozoa and from that of Metazoa. The parallelism between Protozoa and Metazoa is seen when Types 2, 4, and 5 are compared with Type 6.

Type 4 represents a colonial protozoan, such as *Eudorina*. Any and every cell of the colony can divide and form a daughter colony, which can grow to full size and repeat the process. Thus, asexual reproduction by cell division occurs as in the preceding types. The only difference is that the dividing cells of Type 4 do not separate; they remain together and form a colony, the cells of which can again divide to form other colonies. Sexual reproduction occurs when the cells of the colony become macrogametes and microgametes, which unite to form zygotes. Eventually, these zygotes form a new colony by cell division, and so the cycle repeats itself. Since every cell of the colony seems capable of becoming a gamete, there is no distinction between somatic and germ cells. As in Types 2 and 3, every cell of the species is potentially a gamete.

Type 5 represents the cycle in *Volvox*. Asexual reproduction occurs by the division of certain cells, the parthenogonidia, which thus form new colonies, as may each and every cell in *Eudorina*. The more important difference between Types 4 and 5 is that only a few of the cells comprising the *Volvox* colony become gametes, the great majority of the cells continuing as somatic cells which die with the disintegration of the colony after the gametes have been formed and syngamy has occurred. Sexual reproduction occurs by union of aniso-

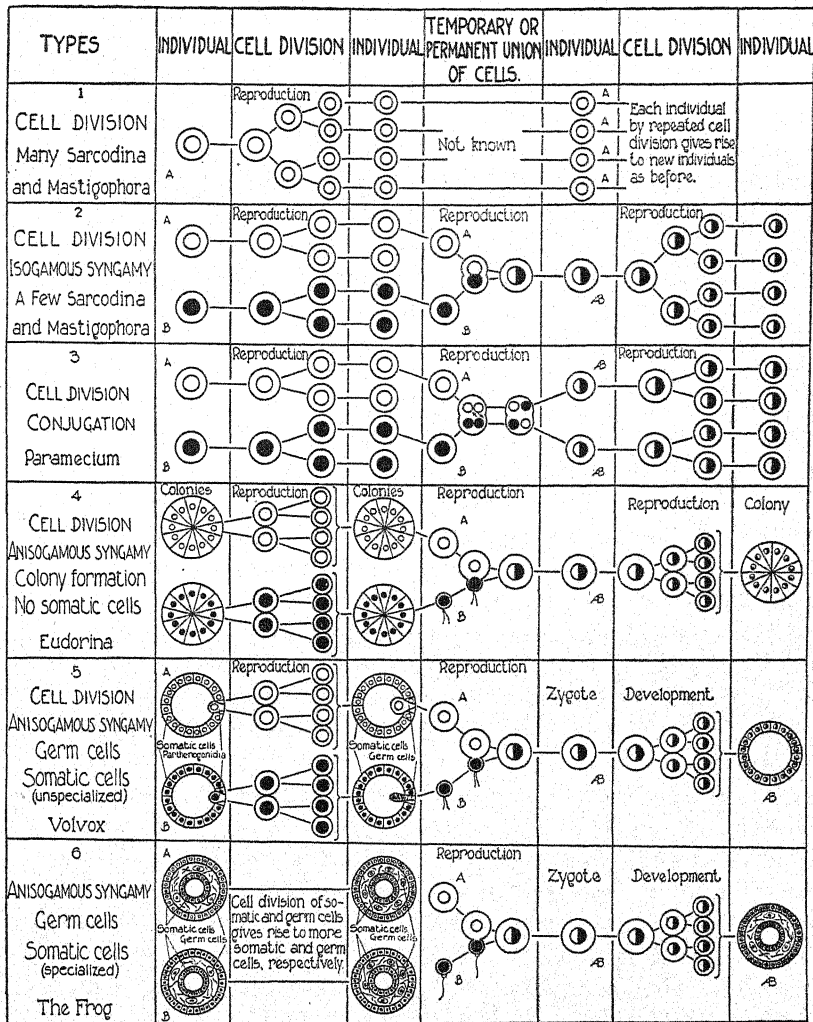


FIG. 194. Comparison of life-cycles in Protozoa and Metazoa. Under *Types* the methods of reproduction are listed first, followed by remarks on cell differentiation and by an example. The letters A, B, and AB, as well as the black, white, and black-white nuclei, are used to indicate the absence of amphimixis in reproduction by cell division and the occurrence of amphimixis in reproduction by syngamy and conjugation.

gametes and in a manner comparable with this process in Type 4. From the resultant zygote a new colony is formed by cell division.

Type 6 represents the cycle in any many-celled animal. For the purposes of the present comparison the only important difference between Type 5 and Type 6 is that in Type 5 there is only one kind of somatic cell, whereas in Type 6 there is more than one kind. If an animal like the frog is being considered, there will be many kinds of somatic cells. Thus, the adult frog can be compared with the colonies shown in Types 4 and 5. In the frog the cell division, by which the zygote develops into the adult animal and any subsequent division of cells, is the part of the life-cycle comparable with the asexual reproduction, or cell division, in Types 1 to 5.

The sexual reproduction of the many-celled animal is, therefore, comparable with the sexual reproduction shown in Types 2, 4, and 5. The same fundamental cycle of cell divisions and syngamy is found from one end of the Animal Kingdom to the other.

By reference to Figure 194 and the points emphasized in the preceding paragraphs, the student should be able to understand and to consider the merits of the following propositions:

1. The *cell division* that constitutes the asexual reproduction of the protozoan is comparable with the cell division that occurs in the development of a metazoan and in the adult metazoan.

2. *Gametes* are found in Protozoa as well as in Metazoa; their union in *syngamy* to form *zygotes* can be compared throughout the Animal Kingdom.

3. A similar basis for *biparental inheritance* exists in Protozoa and Metazoa.

4. The phenomenon of *sex* appears in the Protozoa, since the primary difference between the sexes is the existence of *male cells*, or microgametes, and *female cells*, or macrogametes. The male and female *reproductive organs* and other features which differentiate the sexes of higher animals are secondary developments related to the maleness or femaleness of the gametes.

5. The *individual* is a single cell in such Protozoa as are represented by Types 1 to 3 of Figure 194. In the colonial Protozoa represented by Type 4 there are *individual cells*, associated in *individual colonies*, which do not die a natural death but cease to exist as colonies when the cells separate and go their way independently.

6. In a colony such as Type 5, there are individual cells in individual colonies that are destined to die a *natural death* with the disintegration of the colony; only the gametes are *immortal*, in the sense that they are capable of continuing the species if they unite in syngamy.

7. In Protozoa the cell may *die by accident*; whether it dies of *old age* is a question that is still disputed by protozoölogists. In Metazoa cells may die by accident or in the normal course of events, as do the epidermal cells which die and are sloughed from the human skin; and, as we human beings think so important, the cells of our own bodies and those of familiar animals *grow old* and die a natural death. Hence, in considering the evolutionary origin of Metazoa, it is sometimes said that death was "*the price paid for a body.*"

Other interesting general propositions will occur to the student, notably that such a comparison of Protozoa and Metazoa suggests the steps by which many-celled animals and plants may have arisen from single-celled organisms in the course of evolution when the world of life was young.

The Protozoan Cell

In conclusion the Protozoa are single cells which exhibit the fundamental capacities of metabolism, irritability, and reproduction; they are, therefore, capable of going about the business of living as individuals which are single-celled organisms. An amoeba is, indeed, an animal reduced to very low, if not the lowest, terms. It is true that in some species the protozoan cell becomes multinucleate at certain phases of the life-cycle, but there seem always to be stages of the cycle in which the cell has a single nucleus. In an introductory paragraph it was stated that some zoölogists regard the Protozoa as "acellular" animals. The criticism that can be made of such an acellular theory is twofold. First, the cells of Protozoa have fundamental resemblances to the cells of other animals; second, it seems reasonable to believe that Protozoa and Metazoa both arose by evolution from a common ancestry of single-celled forms. In their descent from such an ancestry the Protozoa have undergone specialization within the limits of a single cell, except as species have arisen which consist of cell colonies (Fig. 190). The Metazoa, on the other hand, have specialized as many-celled animals in which there is a division of labor between the cells and hence an unbalanced physiological state for the individual cell. True, there are species among the Protozoa whose cell organization is far more specialized than that of any metazoan cell, because specialization within the limits of a unicellular state is the unique direction in which the Protozoa have evolved. Yet the most complex of these protozoan cells can be regarded as single cells thus specialized. To regard the Protozoa as animals without cellular organization, and hence to call them acellular, seems unjustifiable and confusing. Unfortunately, there is no fossil record which shows, like the record of

vertebrate evolution, how unicellular and multicellular animals evolved. The record does show that protozoans as specialized as the Radiolaria and Foraminifera have been in existence since the time of the early fossil-bearing rocks. From this fact it can be presumed that there were protozoans æons before that early period, probably before there were any many-celled animals. If we put facts together as in the discussion of colonial Protozoa, it seems reasonable to suppose that the life-cycles of Protozoa and Metazoa are as we now find them because the many-celled and also the single-celled animals of the present day had a common ancestry in unicellular organisms which lived in the remote past. Obviously then, the Protozoa are the simplest of all animals, despite their many specializations as cells, and they seem to be more like the ancestors of all animal life than do any animals now living.

CHAPTER 9

THE SIMPLEST MULTICELLULAR ANIMALS: MESOZOA AND PORIFERA

In preceding chapters the structure and functions of the most complex and of the simplest animals have been examined. The variety and unity in animal life and the principles of classification have been indicated. Between the extremes of Chordata and Protozoa there are many kinds of Metazoa, or multicellular animals. In this chapter the very simplest types of these metazoans will be considered. These simplest of all Metazoa constitute the Phylum *Mesozoa* and the Phylum *Porifera*, two quite different types but each with a very lowly organization.

The Phylum Mesozoa

All Mesozoa are parasites within the bodies of other animals. They may be defined as animals consisting of an outer syncytial or cellular layer, which is commonly ciliated and which encloses one or more cells that give rise to the gametes and to another type of reproductive cell called agametes. The life-cycle is complicated and apparently includes asexual and sexual generations, which alternate. The phylum includes the single Class *Moruloidea*, which includes the Order *Dicyemida* and the Order *Orthonectida*. The members of this phylum are the simplest of all the truly many-celled animals, although this simplicity is perhaps an outcome of degeneration, since all Mesozoa are parasitic during the greater part of their life-cycles. Parasites commonly show structural simplification, as compared with their free-living relatives, and the Mesozoa may have degenerated greatly in the course of their evolution. Such modification may have gone so far that it would be impossible to identify the free-living type from which the Mesozoa have evolved even if this type were still in existence. Many zoölogists regard the Mesozoa as greatly degenerated flatworms (*cf.* Chapter 11), but there is no clear evidence for an evolutionary origin of this sort. When certain forms, which can no longer be so classified, are removed from the phylum, the Mesozoa emerge as a small but well-defined group, which is important because its members possess a simpler or-

ganization than any other such group of many-celled animals. They can, therefore, be taken at their face value as the simplest Metazoa of the present day, even though they may have arisen from more complex ancestors and become simplified as a result of their parasitic existence.

Structure and Life-cycle. The dicyemids, as members of the *Dicyemida* are called, occur as parasites in the excretory organs (nephridia) of squids and devil-fish (cf. Figs. 143 D-G and 324, pp. 224 and 438). They are small, elongated animals which are a few millimeters in length and consist of very few cells, often a total of less than twenty-five (Fig. 195). An outer layer of these cells, which is ciliated, encloses an inner *axial cell* or cells from which the *reproductive cells* arise. The outer, or *somatic, cells* are differentiated into an anterior region, called the *head*, and a *trunk* region. The structure of a dicyemid is thus extremely simple. But the life-cycle is complex and is not known completely for any single species. Apparently, from the single axial cell many cells are formed which are called *agametes*, because they develop without syngamy and cannot be regarded as parthenogenetic ova (cf. p. 130). It is an instance in which a single cell, which may be called a germ cell but is not a gamete, is capable of reproducing the new generation. The details are difficult to observe and are still in dispute among investigators, but it seems that several generations are produced by means of agametes and that free-swimming ciliated larvæ are formed within the parent and liberated. Whether there is a sexual stage while the parasites are living in the excretory organs of the squid is in dispute. If not in the squid, a sexual generation may occur in another host. The full life-cycle is not yet known.

In the *Orthonectidæ* there are asexual phases in the life-cycle; there are also male and female individuals and, consequently, sperm and egg cells which unite in syngamy. Hence one suspects that males and females with their sperm and egg cells may some day be recognized with certainty in the dicyemids.

The Body-plan and Life-cycle. To generalize, the mesozoan body consists of a small number of body cells surrounding a parent germ cell capable of producing many agametes, which are single cells capable of reproducing a new individual. In some and perhaps all species gametes are eventually produced, so that asexual generations alternate with sexual ones. Although the mesozoan is little more complex than some colonial protozoans (cf. pp. 289-290), it is clearly a many-celled animal. Even if its simplicity has resulted from a parasitic mode of life, it is an example of a very lowly type of metazoan. If its simplicity is really primitive and not mainly the result of parasitic life, the

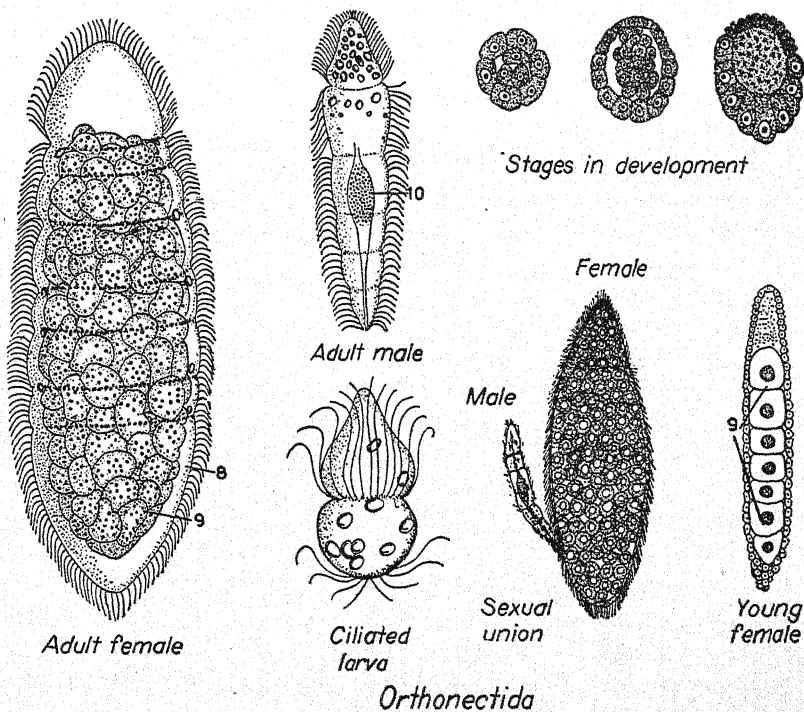
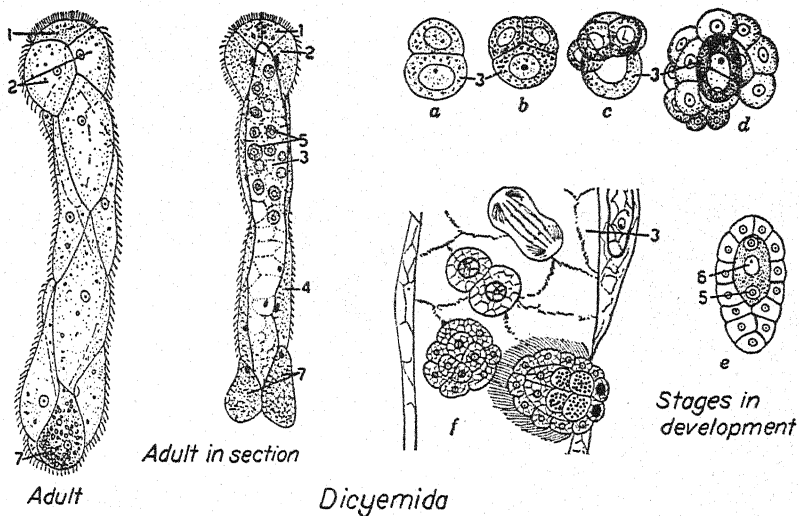


FIG. 195. Representative Mesozoa.

(From L. H. Hyman, "The invertebrates: Protozoa through Ctenophora," copyright 1940, by McGraw-Hill Book Co., reprinted by permission.)

mesozoan type is very important because it suggests a possible step in the evolution of many-celled from single-celled animals.

The Phylum Porifera

The Porifera are the simplest multicellular animals that constitute a well-defined group and include a considerable number of species. They may be characterized as Metazoa with tissues of a very simple sort but without organs, with a more or less extensive system of internal cavities but no digestive cavity, or enteron, and usually with an internal skeleton. The name Porifera, meaning "pore-bearers," is appropriate because there are many small openings upon the exposed surface by which water enters on its way to the internal cavities, and one or more large openings, the oscula, through which this water finds exit.

The Phylum *Porifera* includes three classes: the Class *Calcarea*, in which the skeleton is calcareous and in which are included the simplest sponges, such as *Clathrina*, *Leucosolenia*, and *Grantia* (Fig. 196); the Class *Hexactinellida*, or glass sponges (Fig. 198); and the Class *Demospongiae*, in which are included the bath sponges and related forms (Figs. 199 and 200). In general, the skeletons of sponges are composed of minute spicules, of fibers as in the bath sponge, or of both spicules and fibers (Fig. 197). For example, *Leucosolenia* has a skeleton of calcareous spicules; a glass sponge has siliceous spicules; the bath sponge, *Euspongia*, has a fibrous skeleton; and the fresh-water sponge, *Spongilla*, has a skeleton of both fibers and siliceous spicules. The spicules of sponges are often so characteristic that families and even genera may be identified from spicules alone, which occur, like the shells of Foraminifera (*cf.* p. 251), in the débris upon the bottom of the ocean and are often found in sedimentary rocks. With the exception of a few species that rest upon the bottom, all sponges are firmly attached, but there is a free-swimming, ciliated larva in the early development (Fig. 204). All sponges are marine except the Family *Spongiillidae*, and most species occur in shallow water. Fragments of sponges and sponge spicules occur in pre-Cambrian deposits, and there are many remains in the later rocks (*cf.* Fig. 469, p. 646). At first sponges were classified as plants because of their attachment and manner of growth; later they were regarded as protozoan colonies related to the choanoflagellates, because of their collared cells (*cf.* Fig. 190 C, p. 287, and Fig. 202 B); then they were classified with the coelenterates; and finally they were given their present position as a unique and aberrant phylum. The most familiar example of a sponge

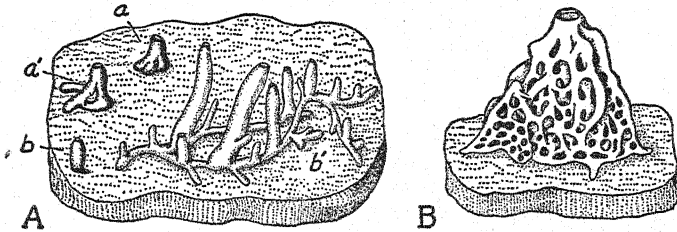


FIG. 196. Calcareous sponges of the ascon type (cf. Fig. 201 A). A, a, and a', young individuals, and b, olynthus of *Clathrina coriacea*; b', colony of *Leucosolenia variabilis*. B, *Clathrina clathrus*.

(Redrawn from E. A. Minchin in E. R. Lankester, "Treatise on zoölogy," copyright, 1900, by A. and C. Black, printed by permission.)

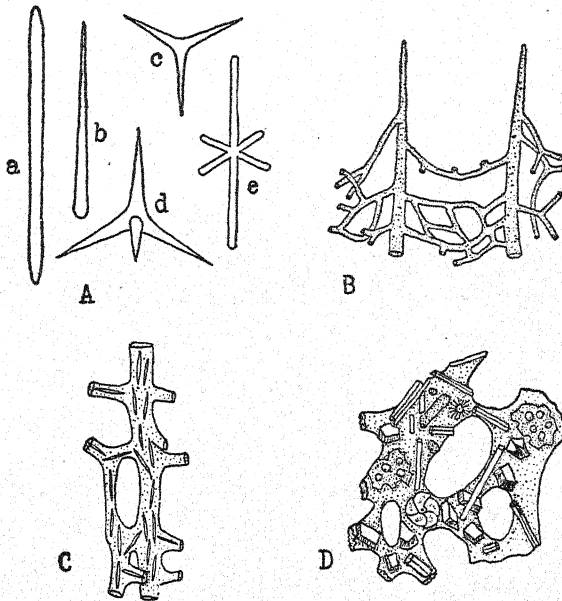


FIG. 197. The skeleton in sponges. A, types of spicules; a and b, monaxon; c, triaxon; d, tetraxon; e, quadriradiate. B, spongin fibers, of *Euspongia*. C, spongin fibers containing spicules, in *Chalina*. D, spongin fibers containing foreign bodies, in *Spongelia*.

(A-C, redrawn from E. A. Minchin, *op. cit.*, printed by permission; D, redrawn from F. E. Schulze, 1879, *Zeitschrift für wissenschaftliche Zoologie*, vol. 32.)

is *Euspongia*, the fibrous skeleton of which is seen as the bath sponge. A sponge of this sort may be regarded as a colony of individuals, although the boundaries of these individuals are indefinite. To understand the organization of sponges, one must begin with forms that are much simpler than any such species as the bath sponge.

General Structure: The Olynthus. The structure of sponges is best explained by first describing the fundamental type from which all sponges have probably arisen in the evolution of the phylum. This type, which is called the olynthus, was originally supposed to be an adult sponge and was then called by the generic name *Olynthus*. It is now known to be a late stage in the development of certain species. An olynthus is a cylindrical organism, attached at its basal end, with an opening, the *osculum*, at its free end, and an inner cavity known as the *cloaca* or *spongocæl* (Figs. 201 A and 202). The walls of this hollow cylinder are perforated by *pores*, through which water enters the cloaca. These pores are intracellular canals in cells called *porocytes*. The external surface and the distal surface of the cloacal cavity are covered with a *dermal epithelium* of flattened cells, and the cloaca is lined with cells called *choanocytes*

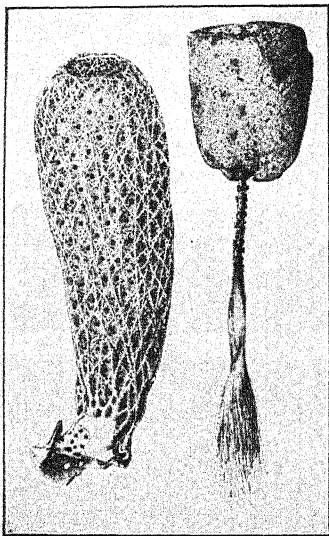


FIG. 198. Glass-sponges. Right, *Regadrella phœnix*; left, *Hyalonema* sp.

(After Agassiz.)

because their flagella are surrounded by collars as in choanoflagellate Protozoa (cf. Fig. 190 C, p. 287). Between the dermal cells and the choanocytes is a middle region containing the skeleton of *spicules* with their secreting cells, the *scleroblasts*, and connective tissue cells, or *collencytes*. The wandering cells called *amœbocytes* are found principally in this region but may occur in any part of the sponge, since they migrate by amœboid movements like the white blood cells of a vertebrate. The *archæocytes*, which are a large type of amœbocyte, are to be regarded as embryonic or totipotent cells (cf. pp. 120, 357, and 460), because they are described as differentiating into all the other cell types, including the egg and sperm cells.

More Complex Sponges. The simplest adult sponges, such as *Clathrina* and *Leucosolenia*, arise by budding and growth from an olynthus

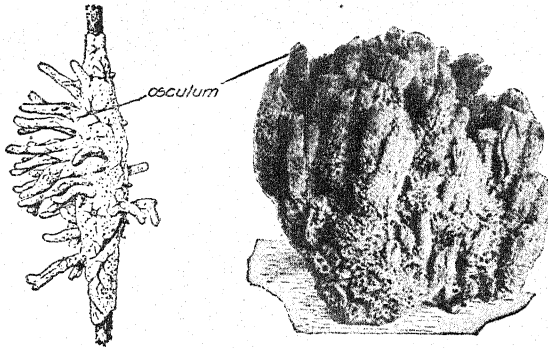


FIG. 199. Fresh-water sponge (*left*) and a bath sponge (*right*).
(*Left*, from W. Weltner, in O. Zacharias, "Die Tier und Pflanzenwelt des Süßwassers," 1891.)

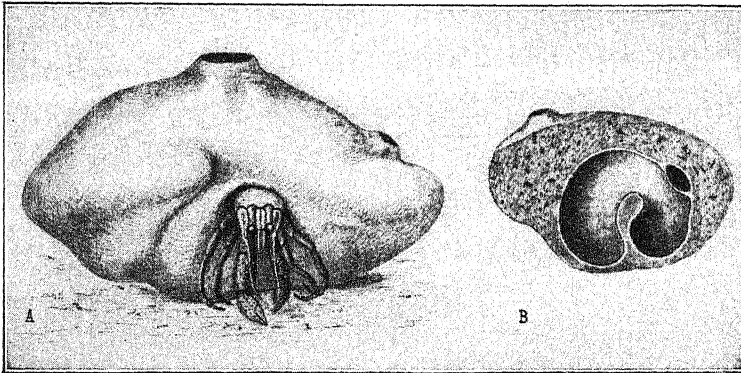


FIG. 200. A crab encased in a sponge. The crustacean, a species of *Pagurus* from Puget Sound, like other so-called "hermit crabs" appropriates the empty shell of a gastropod mollusk. The sponge becomes attached to this shell and grows completely around it, eventually destroying the shell and leaving the crab in a spiral cavity that was originally the cavity of the shell. The association seems to be a normal one and, therefore, a case of symbiosis or living together with mutual advantage, since the crab is protected, and the sponge, which is a sessile animal, is carried from place to place. *A*, the crab exposed as it appears during locomotion, and the encasing sponge, which has two oscula. *B*, the sponge cut open, showing part of the spiral cavity occupied by the crab.

(Drawn by George T. Kline.)

(Fig. 201). More complex sponges are modified in a great variety of ways, but their units of structural organization, the so-called *canal sys-*

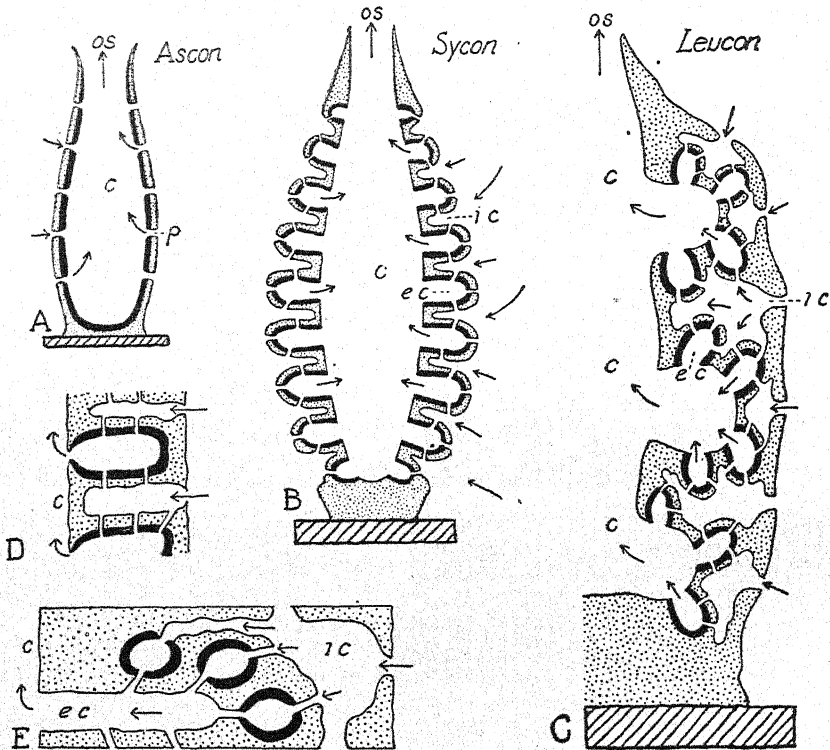


FIG. 201. Canal systems of sponges. A, ascon type. B, sycon type. C, leucon type. D, a portion of the wall of a sponge showing a specialization of the sycon type. E, a portion of the wall of a sponge showing a specialization of the leucon type. In the sycon and leucon types, the openings into the incurrent canals (ic) are called *ostia*; the openings from the excurrent canals (ec) are called *apophyses*; and the openings from the incurrent to the excurrent canals are called *prosopyles* and correspond to the *pores* (p) of the ascon type. The arrows indicate direction of the water currents. c stands for cloaca; ec, excurrent canal; ic, incurrent canal; os, osculum; p, pore.

(Redrawn from E. A. Minchin, in E. R. Lankester, "Treatise on zoölogy," copyright, 1900, by A. and C. Black, printed by permission.)

tems, can be derived from a type like the olynthus in the manner shown by Figure 201. The primary type of canal system found in the olynthus is called *ascon*. This has no complications, except as the cylindrical body of the sponge may form branches of similar structure. A second type, called *sycon* and found in such sponges as *Grantia* and *Sycon*, is

actually derived in development by folding of the wall of an olynthus stage and subsequent differentiation. Additional cavities are thus

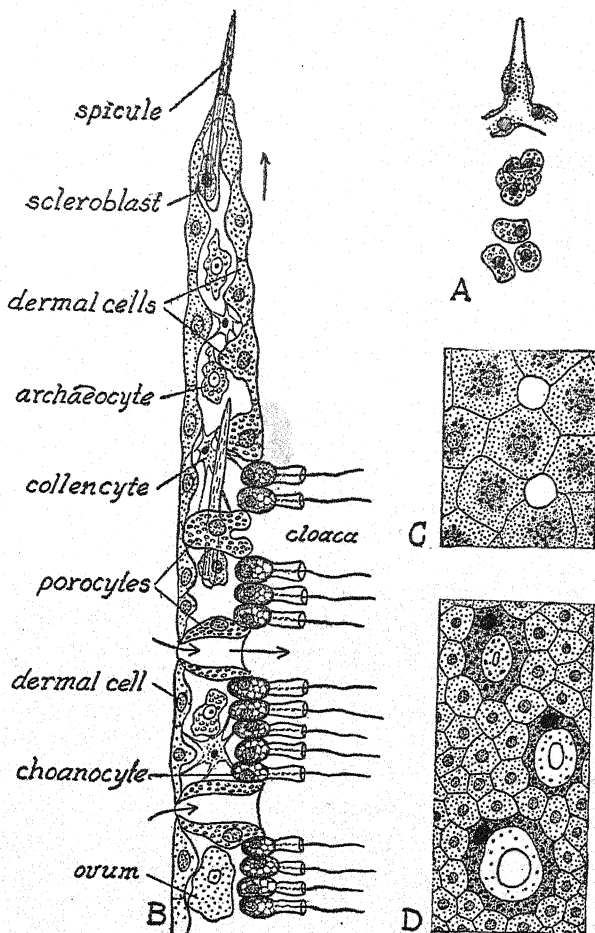


FIG. 202. Cellular structure of an olynthus. *A*, scleroblasts and spicule. *B*, longitudinal section of body wall; arrows indicate the direction of water currents. *C*, external view of body wall, showing pores and dermal cells. *D*, in ternal view of body wall, showing choanocytes and porocytes.

(*A*, *C*, and *D*, redrawn from E. A. Minchin; *B*, based on figure by E. A. Minchin, *op. cit.*, printed by permission.)

formed within the sponge, and the course of the water from the external surface to the osculum becomes more complicated. The openings on the surface of *Grantia* and *Sycon* are not the same as the pores of the olynthus, which correspond to those leading from the so-called *incur-*

rent canals to the excurrent canals. Other changes occur, particularly the restriction of choanocytes to excurrent canals and the extension of the dermal epithelium to line the cloaca; but the homologies between the ascon and sycon types are clear. The third, or *leucon*, type of canal system can be derived from the sycon by folding the wall of the sycon with its two sets of canals. What has been called the *rhagon* type is like a flattened and otherwise complicated sycon. The most highly organized sponges have canal systems that are very elaborate, but all can be compared, in the manner indicated, with the simple arrange-

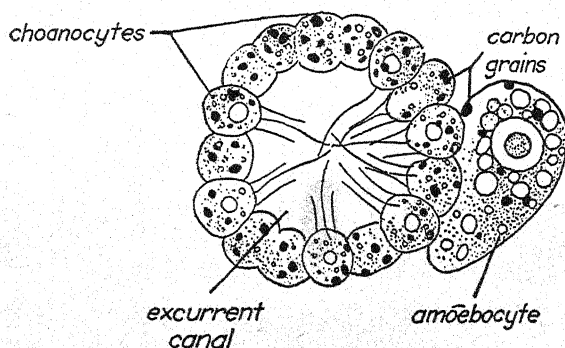


FIG. 203. Amoebocyte receiving carbon grains from choanocytes in a calcareous sponge.

(From L. H. Hyman, "The invertebrates: Protozoa through Ctenophora," copyright, 1940, by McGraw-Hill Book Co., reprinted by permission.)

ment in the ascon. These higher sponges are further complicated by increase in the number of oscula and cloacal cavities, each the center of a canal system, and by the indefinite growth of the whole mass.

Few sponges are symmetrical like *Grantia* and *Sycon*, although the radial symmetry of these genera and of the olynthus appears to be the primitive state from which all sponges have been derived in the evolution of the phylum, if not in the development of the individual. Moreover, there may be great differences in shape among the individuals of the species, because growth of a sponge, like that of a plant with its attached mode of life, is so much influenced by the immediate environment.

Metabolism. The details of ingestion are problematical, although it is clear that the food of sponges consists of microörganisms and organic débris which enter with the inflowing water and become ingested by certain cells. Porocytes, archæocytes, and choanocytes have been described as ingesting such food particles. In view of the rapid growth in many sponges the nutrition must be effective. It is assumed that the

metabolism as a whole is similar to that in other animals where it is better understood.

Precise study of the metabolism of sponges is difficult, as may be imagined if one considers the structure of these animals. When the carbon granules of India ink and other inert substances are added to the surrounding water, some of them enter the surface openings. Later, when bits of the sponge are examined, the granules may be seen as particles ingested by certain of the cells (Fig. 203) in the same manner as such particles are seen after ingestion by a paramecium. Unicellular organisms have been observed being ingested in a similar manner. Digestion is undoubtedly intracellular as in Protozoa. In the calcareous sponges *Grantia* and *Sycon*, the food particles seem first to be ingested by the choanocytes and then passed into near-by amœbocytes. Since the amœbocytes are migratory and capable of differentiation into other cell types, the food may be thus distributed to all parts of the sponge. Food storage of carbohydrates, fats, and proteins occurs in modified amœbocytes. Nitrogenous excretory products have been demonstrated in a few sponges. Soluble excretions and any carbon dioxide would be easily removed by the water current flowing from the osculum. For respiration an abundant supply of oxygen is provided by the inflowing water currents.

Irritability. The flow of water into the minute openings upon the surface, through the canal system to the cloaca, and out the osculum (Fig. 201) is the factor that conditions all other activities of the sponge. Supposedly, this flow is caused by the flagella of the choanocytes, although the manner in which these flagella produce such a steady and relatively strong current is not obvious. The only reactions to stimuli that are easily demonstrable in sponges are the closing of pores and oscula and contractions of the entire mass of cells, which may obliterate the smaller cavities of the canal system. These reactions, which may be local or may involve the entire sponge, are followed by a slow return to the expanded state. In some sponges there are special con-

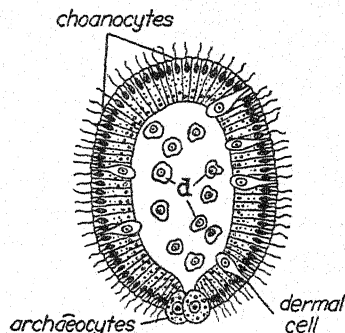


FIG. 204. Ciliated larva of *Clathrina blanca*, showing the future dermal cells migrating into the cavity of the larva; the cavity becomes filled with such cells (*d*), which later pass out to form the outer layer of the adult.

(From E. A. Minchin, in E. R. Lankester, "Treatise on zoölogy," copyright, 1900, by A. and C. Black, reprinted by permission.)

tractile cells (Fig. 206), but there are no nerve cells and no sensory cells. Coördination in the sponges is limited by the absence of receptors

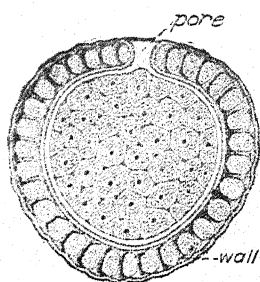


FIG. 205. Gemmule of a fresh-water sponge, *Spongilla fluviatilis*. The gemmule consists of a mass of cells surrounded by a heavy wall containing spicules; the cells escape through the pore and form a new sponge.

(From W. Stempel, "Zoologie im Grundriss," 1926.)

and nerve cells. The individual cells respond directly to stimuli as *independent effectors* because of the irritability of their protoplasm. The relatively slow transmission from cell to cell is known as *neuroid transmission*, in contrast with the nervous transmission by way of neurons, or nerve cells, in more complex animals (cf. p. 71). These limited and sluggish reactions are adequate, since all sponges are either attached or incapable of locomotion in their adult stages.

Reproduction and Development. Most sponges seem to be hermaphroditic, that is, capable of producing both *egg* and *sperm cells* in the same individual, although the eggs and sperms may be produced at different times, thus making self-fertilization impossible. In *sexual reproduction*, the *zygote*, formed by the *syngamy* of egg and sperm, develops within the parent to a *ciliated larva*, which is discharged through the osculum with the outgoing water (Fig. 204). After a brief period of free life, this larva becomes attached and develops with an olynthus stage in the simpler forms and with more specialized stages in the complex sponges. The final stages include much budding and growth if a large mass is formed. This budding is comparable with the *asexual reproduction*, or reproduction by cell division, that occurs in some other many-celled animals (cf. p. 330), although it is often difficult to distinguish from the general process of growth. The fresh-water sponges and some marine sponges form internal buds, called *gemmules*, which are covered with resistant membranes and can survive severe conditions such as drying and freezing (Fig. 205). The so-called *reduction bodies*, which are formed in many sponges under various ad-

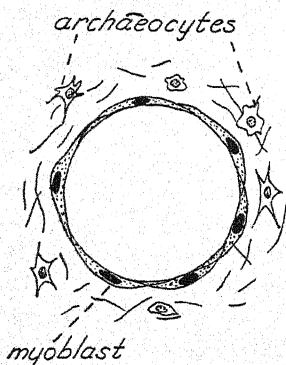


FIG. 206. Myoblasts surrounding an internal opening in a calcareous sponge of the sycon type, *Grantia* or closely related species.

verse conditions, consist of dermal cells surrounding a mass of amoebocytes. These bodies are less resistant than gemmules, but they serve a similar purpose in carrying the species through periods during which normal life would be impossible. With the return of favorable conditions the gemmule or the reduction body can produce the fully developed individual.

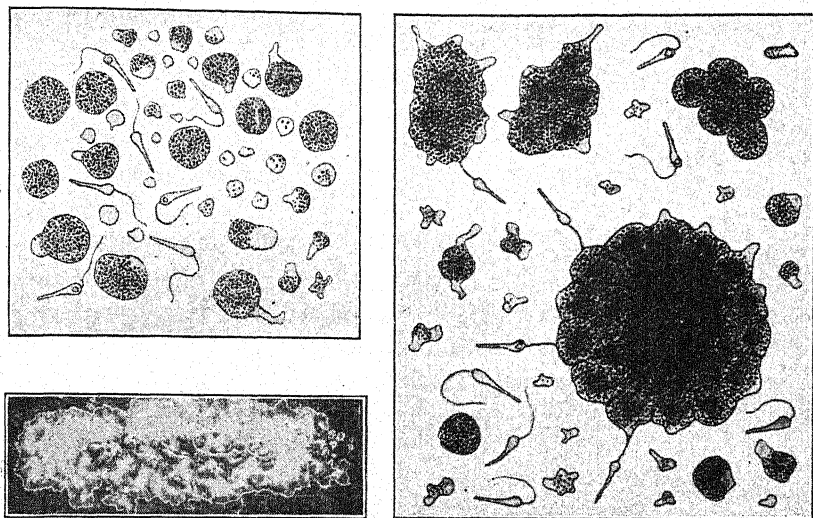


FIG. 207. Dissociation and reassociation of cells in *Microciona*. *Left above*, the separated cells as they appear immediately after passing through the bolting cloth. *Right*, masses formed by reassociation of the cells several hours later. *Left below*, reassociation mass becoming a young sponge some days later.

(From H. V. Wilson, 1910, Bulletin U. S. Bureau Fisheries, vol. 30.)

Regeneration and Reassociation. Regeneration, by which lost parts are restored and even whole individuals formed from small pieces (cf. Fig. 244, p. 353), is commonly associated with conspicuous powers of asexual reproduction. The budding and vegetative growth of sponges would lead one to expect greater powers of regeneration than seem to exist in these animals. Some sponges will regenerate new individuals from cuttings, as do many plants, but in many species the restoration of parts is more limited. The remarkable process of reassociation of cells after dissociation occurs in a few sponges (Fig. 207). For example, pieces of *Microciona prolifera*, the common red sponge of the Atlantic Coast, can be squeezed through silk bolting cloth so that the cells are separated or dissociated. If these cells are allowed to settle upon the

bottom of a dish of sea water and remain undisturbed, they will become reassociated in small spherical masses within 24 hours and then develop as thin encrustations upon the bottom. Under favorable conditions large sponges like the original will eventually be formed. A similar reassociation of dissociated cells occurs in certain coelenterates, but no such phenomena are known in more specialized animals.

The Sponge Body-plan

To speak of the sponge "body" raises the question of what constitutes an individual in the animals of this phylum. In the olynthus or in such a sponge as *Grantia*, an individual with a single osculum is recognizable. In sponges that grow into large masses with many oscula, the entire mass may be called an individual, as a tree with its repetition of parts is so called; or the individual sponge may be defined as any part of the mass that includes an osculum and its related canal system. However one defines the individual sponge, the body-plan that is basic for the phylum is the one seen in the olynthus and its simpler derivatives (Fig. 201). In the cellular organization of the sponge body, there are tissues of a simple sort but no organs, if one means by organs localized groups of tissues that have restricted functions. The early stages of the development are peculiar. Finally, the sponge has no internal cavity homologous with the digestive cavity, or enteron, of other multicellular animals. This last feature of bodily structure, rather than the primitive cellular organization and the peculiar mode of development, gives the phylum its unique position among the Metazoa (*cf.* Fig. 135, p. 215).

CHAPTER 10

THE CŒLENTERATA AND CTENOPHORA

The Phyla *Cœlenterata* and *Ctenophora* are still classified by some zoölogists as two subphyla (Cnidaria and Acnidaria) within a Phylum Cœlenterata. The basis for such a classification within a single phylum is that these two groups of animals have a digestive cavity with but one opening, which functions as both mouth and anus; and that all these animals have two cell layers, being thus diploblastic, although a middle layer of some complexity is found in the more specialized cœlenterates and in ctenophores. Under the single-phylum classification the forms here called Cœlenterata are usually called Cnidaria ("with threads"), whereas the Ctenophora are called Acnidaria ("without threads"), because the Cœlenterata, or Cnidaria, have stinging threads which are not present in the Acnidaria.

The Phylum Cœlenterata

The Cœlenterata are the simplest many-celled animals that possess the digestive cavity characteristic of all Metazoa except the Mesozoa and Porifera. They may be defined as radially symmetrical animals composed of two layers of cells, the ectoderm and the endoderm, and an intermediate region. In the simplest cœlenterates this middle region is non-cellular and no more than a tough membrane; in more specialized cœlenterates it is a thick gelatinous region or mesoglea which may contain so many cells that it constitutes a third layer comparable to a simple type of mesoderm. The digestive cavity has but one opening, which functions as both mouth and anus and is usually surrounded by tentacles. The organs and systems that occur are simple in structure and function. As compared with sponges, the cœlenterates exhibit a more definite form and symmetry. The name Cœlenterata, which means literally "hollow intestine," was presumably suggested by the resemblance of forms such as the fresh-water hydra to a piece of the intestine in higher animals. The phylum includes three

classes: the Class *Hydrozoa*, or hydras, hydroids, hydroid jellyfishes, and hydroid corals; the Class *Scyphozoa*, another type of jellyfishes; and the Class *Anthozoa*, or sea-anemones, sea-pens, sea-fans, and true corals.

The great majority of cœlenterates are marine. They occur at all depths in the ocean and under a wide range of conditions, since the phylum includes both attached and free-living species. They are, however, predominantly inhabitants of the shallow waters along shore and the upper layers of the deeper ocean. In their feeding habits they are strictly carnivorous; they capture other animals by means of their tentacles and microscopic bodies called nematocysts, from which the stinging threads are everted. Most cœlenterates are attached for a considerable part of the life-cycle, during which they commonly reproduce by budding or fission. Thus, colonies of innumerable individuals may be produced, as in corals. In some species there is an alternation of attached and free-living generations. The radial symmetry so characteristic of the phylum is presumably related to the attachment, since it is a rule that attached animals have at least some degree of radial symmetry.

The attached mode of life and the radial symmetry led early naturalists to classify the cœlenterates as plants. Their animal nature became apparent when it was discovered that they have tentacles, mouths, and digestive cavities. They were then classified with the echinoderms in a group called the Radiata (*cf.* Fig. 512, p. 699). Finally, when it was shown that the structure of cœlenterates is quite different from that of echinoderms, the Phylum Cœlenterata was established. Remains of cœlenterates such as hydroids and corals appear in the earliest fossil-bearing rocks and in many later deposits. In a few instances even jellyfishes seem to have left a record as imprints made upon ancient beaches and preserved like leaf impressions (*cf.* Fig. 471 A, p. 650). The coral polyps have played an important role in geologic history.

The fresh-water hydras, which have long been studied by zoologists (Fig. 209), are widely distributed and fairly representative cœlenterates. They are also representative of all the Metazoa higher than sponges in so far as they have a digestive cavity and cell layers that may be compared with these parts in higher Metazoa. Perhaps no animal is better suited to illustrate the structure of a metazoan reduced to simple terms. We shall, accordingly, examine the hydra as a cœlenterate, but more particularly as a simple metazoan to be compared in structure and function with the vertebrate and the protozoan.

The Class Hydrozoa

The Hydra: *Habitat and Activities.* Two species of the Genus *Hydra* are common in the eastern and central United States: *Hydra americana*, which is gray or sometimes tan; and *H. carnea*, which is brown and has very long tentacles. *Chlorohydra viridissima*, a green hydra, is often found. In the Genus *Pelmatohydra* the body is divisible into a proximal stalk and a stouter distal region. *Pelmatohydra oligactis* is widespread, is brown in color, and has very long tentacles. The account that follows is sufficiently general to be applicable to any of these types, unless otherwise stated. The green hydras are smaller and more active, have shorter tentacles, and are likely to be found in greater numbers. The brown hydras are sluggish, but their larger size renders them more favorable for study of the general organization. The individual is found attached to submerged objects by its base and with its body extending into the water, save in exceptional conditions when it may float freely. In an aquarium it is often found attached to the surface film, hanging down into the water. The green

hydra extends its body and frequently changes its position; the brown hydra is more likely to remain with tentacles irregularly extended and almost motionless for much longer periods. These different degrees of activity are correlated with the feeding habits of the two species. As may be observed in the laboratory, hydras devour small organisms, such as water-fleas and minute insect larvæ, sometimes overpowering and ingesting objects much larger than themselves. They will also feed upon bits of meat and similar materials brought in contact with their tentacles (Fig. 208). Although there are no special organs of locomotion, the animal shifts its position by simple movements of the body (Fig. 210) and by a slow gliding of the base without detachment from

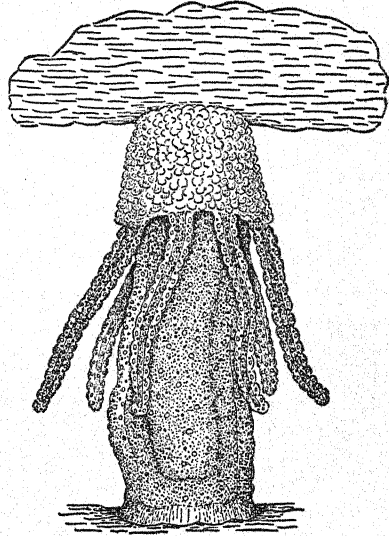


FIG. 208. *Hydra*, with portion of body turned inside out in attempting to ingest a piece of meat.

(From a student's drawing.)

the substratum. Hydras react positively to light of moderate intensity and so tend to collect in the best-lighted part of an aquarium. This reaction is especially noticeable in the green hydras. Before undertaking a further description of habits and general behavior, it will be necessary to describe the structures involved.

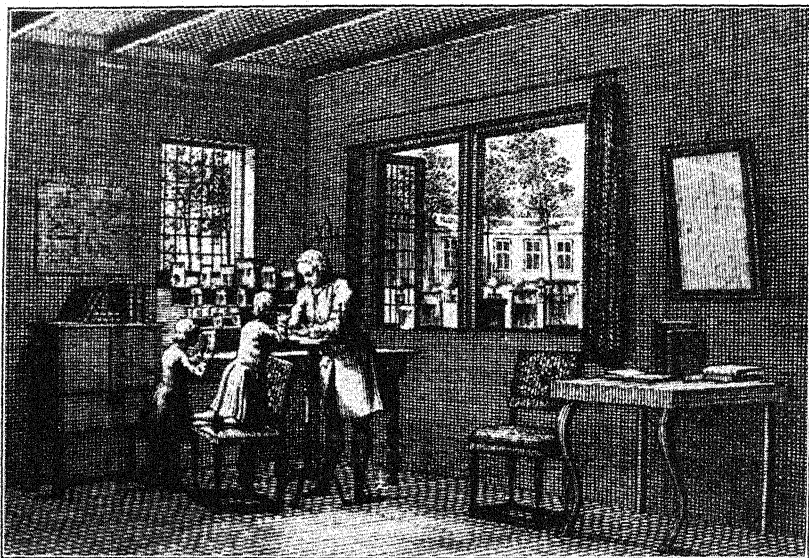


FIG. 209. Vignette from Trembley's monograph on *Hydra*. The author, who was tutor to the sons of an Englishman resident at The Hague, is shown exhibiting hydras to his pupils. He studied the structure, activities, and regeneration of the hydra and concluded that it was an animal, although he first thought it a plant.

(Reproduced from the original by Abraham Trembley, "Polypes d'eau douce," Leyden, 1744.)

General Structure. The hydra consists of an elongated *body* normally attached at one end, the *base* or *foot*, and surmounted at the other by a circle of *tentacles* enclosing a conical region, the *hypostome*, at the apex of which is the *mouth* (Fig. 211). The tentacles vary in number in different individuals as well as in different species. The body and tentacles consist of but two layers of cells surrounding a central digestive cavity, the *enteron*. Between these layers of cells, known respectively as the *ectoderm* and *endoderm*, is the *supporting lamella*, which is apparently a secretion produced by the basal ends of the cells. In jellyfishes there is a thick, gelatinous middle region, containing scattered cells and fibers and called the *mesoglea*. The sup-

porting lamella of the hydra is comparable functionally with an elastic skeleton, because it serves as a place of attachment for the cells and their muscle processes and gives support and continuity to the entire organism. In contrast with most familiar animals, which are bilaterally symmetrical, the hydra is *radially symmetrical*. This is one of the most obvious characteristics of the Cœlenterata, whether attached or free-living.

Cellular Structure and Functions. The *ectoderm* is the outer layer of cells (Figs. 211 and 213) and is composed principally of *large ecto-*

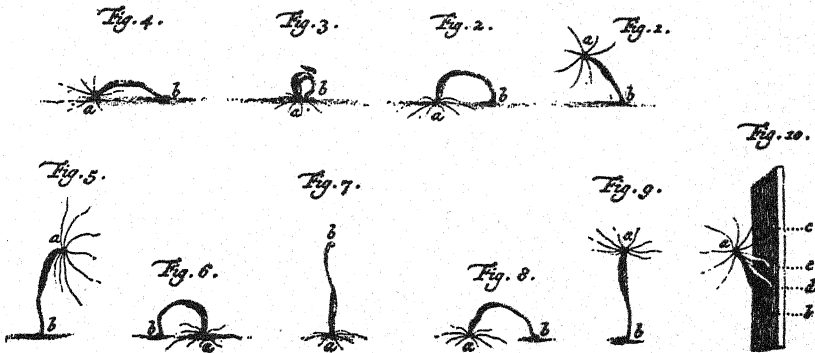


FIG. 210. Locomotion in *Hydra*.

(From one of the plates in Trembley, *op. cit.*)

derm cells, called epithelio-muscular cells because they cover a surface and have muscle processes extending along the supporting lamella. Since these processes all run lengthwise, their contraction shortens the tubular body. The corresponding muscle processes of endoderm cells run transversely and therefore extend the body. The many changes of shape and position exhibited by the hydra are all produced by the coördinated and localized contractions and relaxations of this simple musculature. At the base of the body the ectoderm cells are modified as gland cells that produce the secretion by which the hydra attaches itself. Between the large ectoderm cells of body and tentacles are many small *interstitial cells* and the cells called *cnidoblasts* or *nematocytes*. The *sensory cells* and *nerve cells* of the ectoderm will be described in discussing the capacity of irritability.

Scattered throughout the ectoderm, but most abundant upon the tentacles, are the cnidoblasts containing the *nematocysts*, with which the hydra paralyzes its prey (Fig. 212). Nematocysts are one of the most remarkable mechanisms in the Animal Kingdom. They are not cells but non-living cell products which might be compared to harpoons

ready to be shot from a gun, which is analogous to the cell that has produced them, and capable of paralyzing the hydra's prey. Other coelenterates overpower their prey in a similar manner. Although their bodies are soft and defenseless, save as they can be withdrawn into a

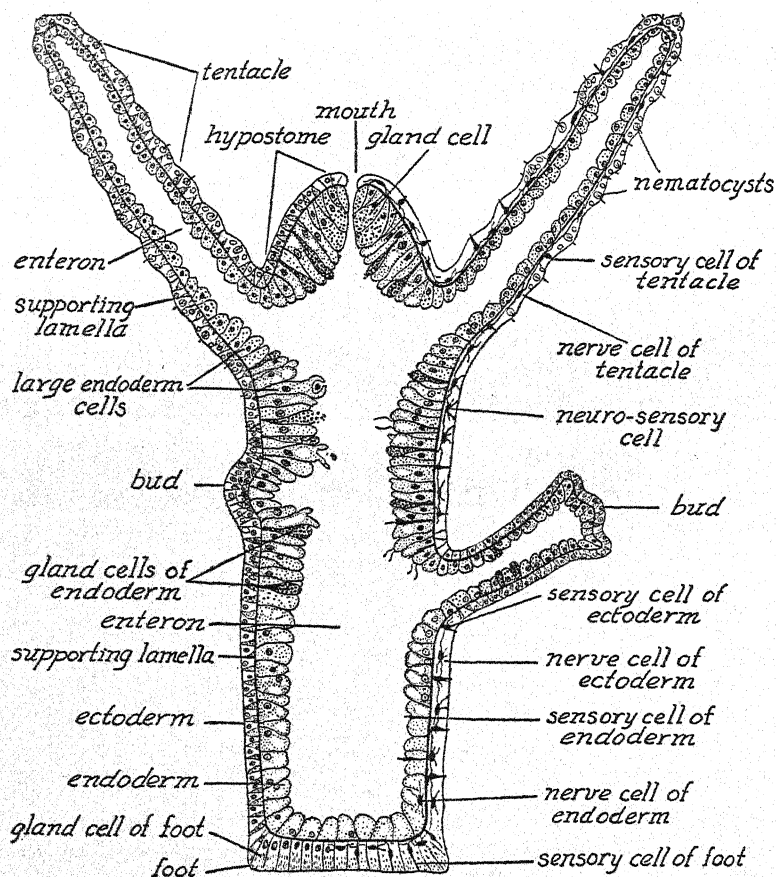


FIG. 211. *Hydra* in longitudinal section to show the cellular structure; diagrammatic.

protecting skeleton, the members of this phylum are terrible enemies of the many animals upon which they feed. The nematocysts of most coelenterates are *not* harmful to man, although they may be irritating. The poison of a few species can induce a violent reaction of the human skin, serious general symptoms, and even death.

In the development of a nematocyst, an interstitial cell produces in its cytoplasm a structure which has at first the appearance of a

vacuole and which is seen later to be a minute capsule containing a thread that becomes surrounded by a densely staining fluid. The details of this development are not fully understood because of the minute size of these early stages. The commonly accepted theory is that the thread, which is hollow in its final stage, arises as an ingrowth from one end of the capsule. Clearly, the nematocyst is not a cell, but a capsule containing an inverted thread and produced within the cytoplasm of a modified interstitial cell, called a *cnidoblast*. The discharge consists of the eversion of this thread, like the turning right

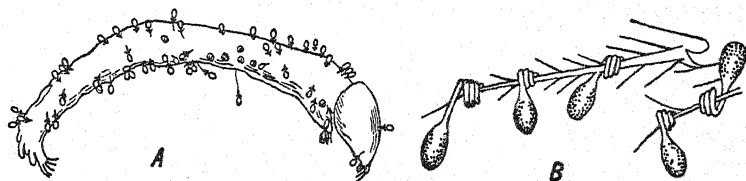


FIG. 212. Nematocysts of *Hydra*. *A*, insect larva punctured by numerous nematocysts of the barbed type. *B*, part of an appendage of a water-flea, showing another type of nematocyst that seems to function like a grappling hook.

(*A*, redrawn from H. S. Jennings, "Behavior of the lower organisms," copyright, 1906, by the Columbia University Press, printed by permission; *B*, redrawn from O. Toppe, 1909, *Zoölogischer Anzeiger*, vol. 33.)

side out of an inturned glove finger. The most probable explanation for this eversion is that water enters the capsule suddenly, resulting in a greatly increased osmotic pressure.

The cnidoblasts may be differentiated from the interstitial cells in a part of the animal remote from the places where nematocysts are most commonly used. In that case the cnidoblast is transferred a considerable distance, as from body to tentacles (Fig. 214). In its final state the cnidoblast has a triggerlike projection, the *cnidocil*, which protrudes from the surface of the ectoderm and is, presumably, the part sensitive to the external stimuli.

Cnidoblasts seem to be *independent effectors*, that is, structures responding directly to stimuli and not under nervous control (Fig. 217). Cnidoblasts and nematocysts are little affected by mechanical stimuli, such as the rubbing of a tentacle with a fine glass rod, or by the movements of the protozoans often found living upon the surface of the hydra. On the other hand, suitable chemical stimuli may be very effective in bringing about the discharge of nematocysts. In nature the nematocysts seem to be discharged through stimulation of the cnidocils by a combination of the mechanical disturbance caused by the prey

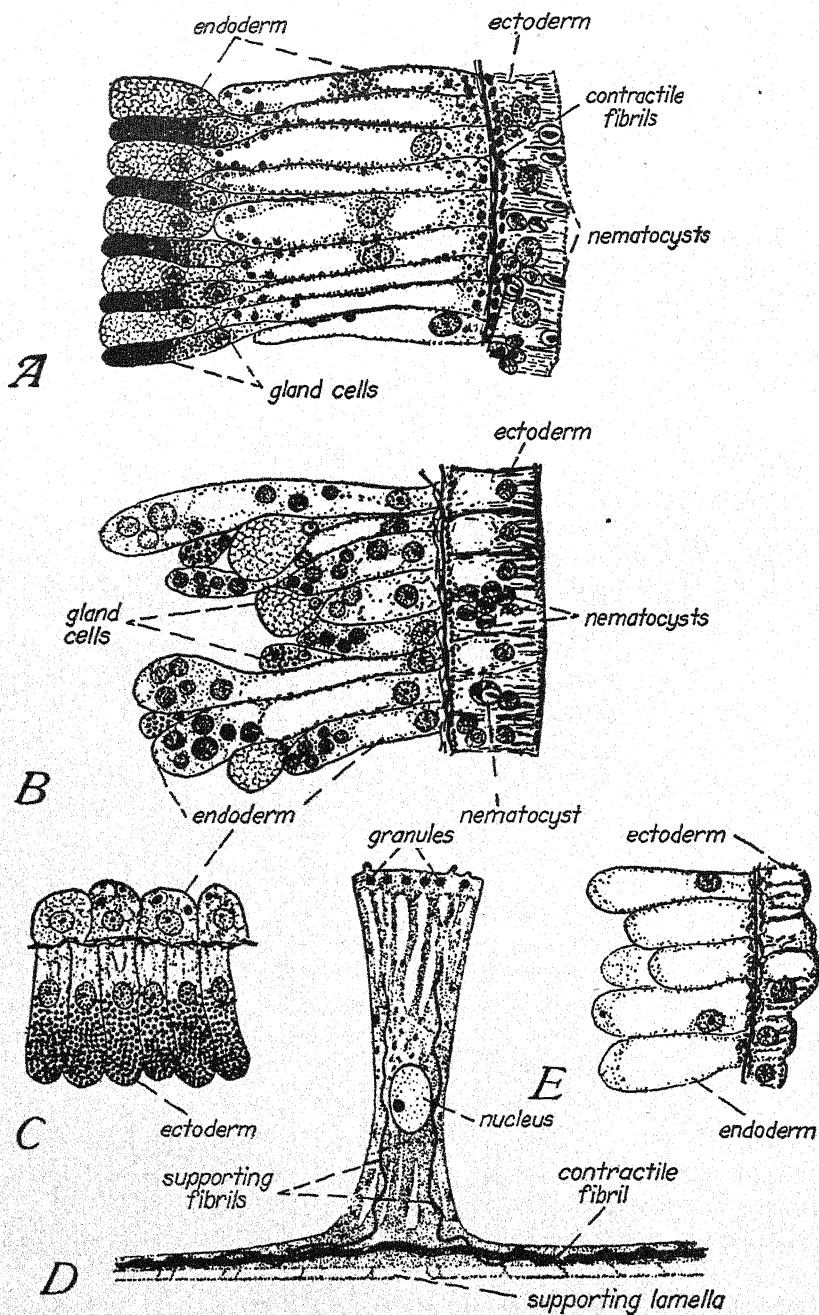


FIG. 213. Cellular structure of *Hydra*. A, from section through the hypostome. B, from section through distal body (stomach) region. C, from section through foot region. D, a large ectodermal cell. E, from section through proximal body (stalk) region.

(After L. H. Hyman, "The invertebrates: Protozoa through Ctenophora," copyright, 1940, by McGraw-Hill Book Co., printed by permission.)

and the chemical substances that diffuse from prey to water. In contrast to the reaction of the cnidoblasts as independent effectors, the muscular responses of the tentacles, in the capture of prey and otherwise, appear to be coördinated by nerve cells, which are numerous in the ectoderm and present in smaller numbers in the endoderm (Figs. 216 and 218).

In hydras there are four types of nematocysts: a large globular type with conspicuous spines on the enlarged basal portion of a long thread, a small globular type with a thread that is spirally coiled after discharge, and two small elongated types with long straight threads. Examination of animals paralyzed by hydras indicates that the threads of the first type can penetrate the body of the prey, and that the threads of the second type can wrap themselves about fine projections, such as the hairs of a water-flea, and thus function like grappling organs (Fig. 212). In some manner the nematocyst carries a poison which paralyzes the prey. The exact nature and location of this poison have not been ascertained. It has been described as being ejected from the free end of the thread and as being located on the outside of the everted thread.

The *endoderm* is the inner layer of cells that lines the enteron. It consists principally of large *endoderm cells*, which may bear one or two flagella and which can put forth pseudopodia at their free ends to ingest food particles (Figs. 211 and 213). Since these cells form a continuous layer and have muscle processes extending from their basal ends, they are epithelio-muscular in character. In contrast with the ectodermal arrangement, the endodermal muscle processes run transversely and so provide a circular musculature by means of which the hydra extends its body. As there are no muscle processes on the endoderm cells of the tentacles, these parts are elongated by pressure of fluid forced into them from the enteron of the body. In green hydras the endoderm cells are crowded with green bodies, which are regarded as unicellular plants. These cells live within the endoderm of the hydra and pass from one generation to the next by transfer in the hydra's eggs. Similar plant cells are found in the endoderm of marine coelenterates, particularly some of the corals. The presence of such cells seems advantageous to the hydra, because green plants take in carbon dioxide and liberate oxygen. Living within an animal's body seems advantageous to the plant cell because animal protoplasm liberates water, carbon dioxide, and nitrogenous products of dissimilation which can be used by a green plant. A relationship of this sort, in which organisms are associated to their mutual advantage, is called *symbiosis*. It may be contrasted with *parasitism*, in which the advantage is all

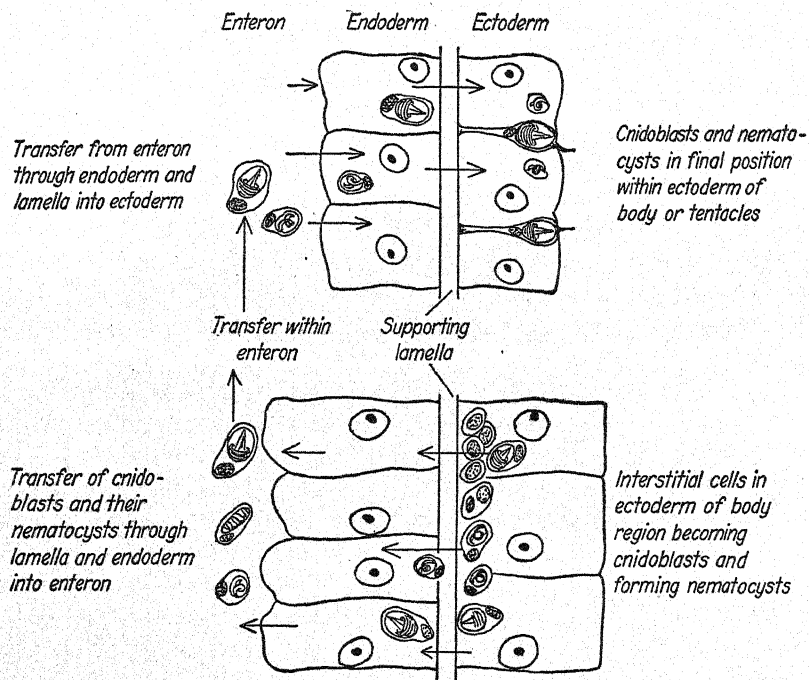


FIG. 214. Origin and transfer of nematocysts in the hydra; schematic. It is possible that, in addition to the method of transfer here shown, there is some transportation of nematocysts by amoeboid movement of the cnidoblasts within the ectoderm.

(Based upon C. S. Jones, 1941, Jour. Experimental Zoölogy, vol. 87.)

on one side, and with *commensalism*, in which two animals are associated as "messmates," without obvious advantage or disadvantage on either side. The Protozoa of the Genera *Trichodina* and *Kerona*, often seen upon the outer surface of hydras, are probably commensal with the hydras and are not true parasites.

In addition to the large cells that compose the greater part of the endoderm, there are *gland cells*, which are club-shaped with the smaller end attached to the basal membrane and the larger exposed to the digestive cavity. They are located principally in the distal third of the body and apparently secrete digestive juices effective in the extracellular digestion that occurs in the enteron. A circle of gland cells within the mouth secretes something which seems to activate the other gland cells, so that the steps in digestion may be more complicated than might be supposed. Scattered *sensory cells*, *nerve cells*, and some *interstitial cells* also occur in the endoderm.

The cells that have been described in the ectoderm and endoderm are collectively known as the *somatic cells*. Cell specialization in hydras gives rise to different kinds of somatic cells but to few that can be compared to the tissues of the frog (*cf.* Fig. 90, p. 149). Since the ectoderm and endoderm cells combine epithelial and contractile functions, the gland cells are the only strictly epithelial cells, although they are scattered and not arranged in a compact epithelium. Thus, there are different kinds of cells, but the differentiation of tissues is on a very low level. Organs are similarly restricted; only the tentacles can be called organs.

Hydras have a considerable number of embryonic or *totipotent cells*, the interstitial cells, which become specialized in different ways throughout the life of the individual (*cf.* pp. 120, 357, and 460). The replacement of cnidoblasts, which disintegrate after their nematocysts are discharged, is by continued differentiation from interstitial cells. Similarly, interstitial cells are important in the differentiation of a new hydra arising by budding and in the production of the *germ cells*, which appear at certain seasons. For all its simple organization the hydra, with its several kinds of somatic cells and the diploblastic body-plan, shows a great advance in cell specialization over such forms as *Pleodorina* and *Volvox* (Fig. 193, p. 291), in which all the somatic cells are alike; and the hydra is more specialized than a mesozoan (Fig. 195, p. 299) or a sponge (Fig. 201, p. 304).

Metabolism. After being paralyzed and held fast by the nematocysts, the small animals that serve as food for the hydra are brought to the mouth by the tentacles and *ingested* by engulfing movements of the hypostome. Soon after this ingestion the food is shifted by

peristaltic contractions of the body to a position in the distal half of the enteron, where the early stages of digestion occur. As the food mass is never found at proximal levels, there is apparently a physiological division of the enteron into gastric and intestinal regions, although no structural difference exists, except the abundance of gland cells in the endoderm of the gastric region.

If the objects ingested as food by a hydra are examined during the earlier stages of digestion, they are found disintegrating in the same manner as food in the stomach of any carnivorous animal. The softer parts of a water-flea become liquefied and divided into particles, while fragments of the indigestible skeleton remain, as would bits of a crayfish skeleton within the stomach of a frog. Eventually, these indigestible portions are *egested*, slowly or by a violent contraction, through the mouth. It is evident that a digestive process takes place within the enteron. This *extracellular digestion*, as it may be called, is brought about presumably by enzymes, since these are known to be the active agents in all animals from which digestive fluids have been obtained in sufficient quantity for experimentation. The endodermal gland cells appear to be the source of these enzymes. The fluid material that results from this digestion within the enteron is presumably *absorbed* by the endoderm cells, and thence by the ectoderm, in a manner comparable with the absorption of digested food by the mucous membrane and underlying cells of a vertebrate. In addition to the extracellular process, there is a process of *intracellular digestion*. The amoeboid activities of the free ends of the endoderm cells include the engulfing of small particles that result from the disintegration of the food mass. Within the *food vacuoles* thus formed, the final stages in the digestion of these particles occur in a manner comparable with what occurs in the food vacuoles of Protozoa.

Thus the food is digested and enters the protoplasm, where it is *assimilated*. There is no circulatory system, but the food in later stages of digestion is distributed to all parts of the enteron by the flagella of the endoderm cells and by the movements of body and tentacles. In this manner a bud (*cf.* Fig. 211) receives food before its mouth is formed. In colonial cöelenterates, such as the hydroids (Fig. 221), this transfer of food to remote parts of the colony is more obviously comparable with the function of a circulatory system in the transportation of nutrients. The enteron of a cöelenterate is sometimes called the *gastro-vascular cavity*, because it has this double function of digestion and circulation.

The protoplasm of hydras, like that of other animals, must be supplied with oxygen. *Respiration* apparently occurs in the hydra by dif-

fusion of oxygen into the cells from the surrounding water. *Dissimilation* occurs in the protoplasm with the formation of water, carbon dioxide, and nitrogenous compounds as in a vertebrate. The *excretion* of these waste products of dissimilation probably occurs from the surface of the hydra, unless certain inclusions found in cells of the endoderm represent accumulations of inert excretory products that are eventually discharged through the enteron and mouth. The observations and experiments that can be easily made upon an animal as small as the hydra, therefore, confirm the assumption that the general protoplasmic requirements are the same throughout the Animal Kingdom. A summary of digestion, absorption, assimilation, dissimilation, and excretion given for a vertebrate (cf. pp. 52-54) serves as a summary of these metabolic changes in a hydra, if the fundamental aspects are considered.

Irritability. All movements of the hydra are the result of contractions by the longitudinal and circular muscle processes. The fact that these processes can contract and relax locally as well as over the entire body and that they react in a coordinated fashion is evidenced by the varied positions and shapes the animal may assume. In addition to extensions and contractions of body and tentacles as a whole, there are peristaltic movements, by which the food is passed from one part of the enteron to another. These may be very slow, consuming from 15 to 30 minutes in traveling over the length of the body, or they may be rapid, as when fecal matter is violently egested or food quickly shifted toward the middle of the animal. The circular muscle processes function as sphincters about the mouth and at the base of each tentacle. Detachment of the base during locomotion seems due to muscular contraction.

Locomotion is effected in a variety of ways (Fig. 210). A hydra may move by imperceptible degrees, gliding upon its base. It may extend itself laterally until the tentacles are in contact with the surface, release the base, which is then drawn to a new point of attachment, and extend the tentacles once more, repeating the process. Again, the hydra may attach the tentacles, release the base, and move by slow somersaults. It can also walk clumsily upon its tentacles with the body free and contracted. Hydraz often float hanging in the water with the base attached to the surface film and sometimes float suspended in the water without such attachment.

In feeding, the activities of green and brown hydraz differ markedly. A green hydra that has not fed for a time will extend the body and tentacles but will remain in one position for only a short period. Failing to secure food, the animal contracts and extends its body at

a new angle. This process is repeated until the area within reach of any one point of attachment has been irregularly covered. An almost imperceptible gliding on the base may occur during these activities and thus new territory be reached. If no food is obtained as a result of these lesser activities, the hydra begins looping, and later it begins to somersault, finally coming to rest if no food is obtained. In contrast with these activities of the green hydra, the brown and gray species remain motionless for considerable periods with the tentacles widely extended, as a fisherman might set out lines in all directions

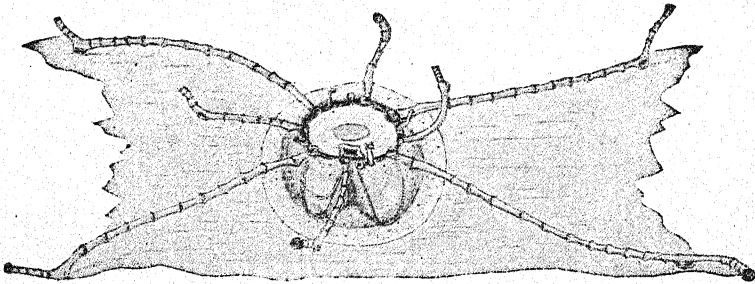


FIG. 215. A young jellyfish, *Gonionemus*, resting upon the bottom with its oral side uppermost.

(From H. F. Perkins, 1902, Proceedings Academy of Natural Sciences, Philadelphia.)

from a boat and wait for a catch. If no food is secured, the animal begins to move after the manner of green hydras. Hungry hydras may go to the bottom of an aquarium and gorge themselves with ooze. This seems to be an alternative means of nutrition not commonly recognized.

The action of the nematocysts in paralyzing and grappling prey has been described. When a water-flea has been thus caught by a single tentacle, the remaining tentacles usually take part in the transfer of the prey to the mouth by coördinated reactions. It is possible, however, for a very small animal to be caught by one tentacle alone and passed to the mouth without reactions by the other tentacles. In either case, the prey is drawn toward the mouth, which may open in advance of the actual contact. When food begins to enter the mouth, the tentacles cease to function. If the food masses are large, the tentacles become folded back from the hypostome, and the final stages of ingestion are accomplished by engulfing movements whereby the mouth "creeps" around the food. A hungry hydra will sometimes ingest animals and bits of meat larger than itself; or, in attempting the impossible, it may turn the body inside out for a short distance (Fig.

208). The coördination shown by the tentacles and the hypostome in the reactions that have been described is accounted for by the nervous mechanism described in a later section. The influence of the physiological state upon the hydra's behavior is shown by the fact that individuals kept for a time without food are much more responsive in their feeding reactions than those that have recently fed.

Study of the responses to specific stimuli reveals that the hydra reacts to mechanical contacts, light, heat, electricity, and chemical substances in solution. The stimuli to which it reacts in the forms of behavior that have been described are probably combinations of such specific stimuli plus the factor of the physiological state of the individual at any given time. These responses to combinations of stimuli can be more easily studied in some of the larger coelenterates. The jellyfish *Gonionemus*, for example, reacts moderately to mere contact with objects, to objects in motion, and to chemical compounds such as acids in solution, but the reaction is greater when these stimuli are combined. Thus the tentacles of a resting *Gonionemus* are somewhat sensitive to the contact of a fine pipette that merely touches them or that is moved along their surface, and to meat juice that is gently ejected against them without movement of the pipette (Fig. 215). But, when the mouth of the pipette is drawn rapidly along a tentacle as the meat juice is ejected, the whole animal goes into action. All the tentacles twist and turn, bending toward the mouth, the hypostome bends toward the tentacle stimulated, and nematocysts are discharged. Presumably this combination of stimuli is like that received from a small fish or crustacean, for the reactions are similar in the two cases.

The cellular organization of the *sensory-neuro-muscular mechanism*, which is the basis for the reactions that have been described, may now be examined. The ectoderm contains many *nerve cells*, or neurons, and at least four different kinds of *sensory cells*, all connected with the muscle processes of the large ectoderm cells (Figs. 216, 217, and 218).

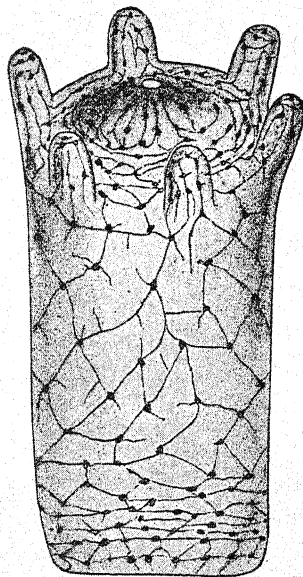


FIG. 216. Young *Hydra*, stained to show network of ectodermal nerve cells and their ringlike arrangement in the foot and hypostome.

(From J. Hadzi, 1909, *Arbeiten zoologischen Institut Wien*, vol. 17.)

In addition, there are *neuro-sensory cells*, so-called because they resemble nerve cells and have processes extending to the outer surface of the ectoderm and presumed to be sensory. The endoderm contains nerve cells and sensory cells, although in much smaller numbers than the ectoderm (Fig. 218 B and C). Slight concentrations of nerve cells in the region of hypostome and base, respectively, resemble the ring-like groupings of nerve cells which occur in more specialized cœlenterates, such as the jellyfishes, and which suggest the beginnings of a central nervous system. This neural mechanism of hydra, which is essentially like that found in other cœlenterates, is described in some detail because it represents a primary level of neural organization.

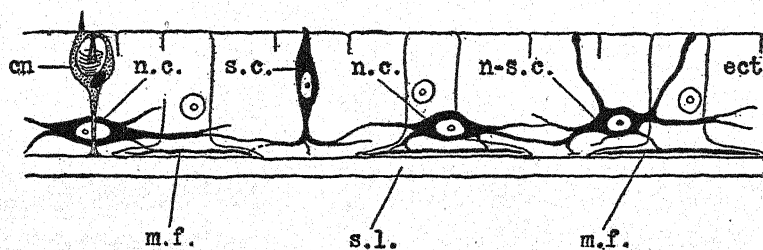


FIG. 217. Diagram of the sensory-neuro-muscular mechanism of *Hydra*. One of the cnidoblasts (*cn*), which are independent effectors, is included. *ect*, ectoderm; *m. f.*, muscle fibril of large ectoderm cell; *n. c.*, nerve cell; *n-s. c.*, neuro-sensory cell; *s. c.*, sensory cell; *s. l.*, supporting lamella.

The ectodermal nerve cells of hydra and other cœlenterates have long been described as constituting a network, because the cell processes have been supposedly continuous from cell to cell. It will be recalled that the nerve cells of higher animals are not thus continuous but are in contact through the so-called *synapses* (*cf.* p. 70). It now appears that synapses may occur in certain cœlenterates, although critical observations are well-nigh impossible in a form like hydra. The accompanying figures were drawn on the assumption that the cells of the entire neuro-sensory system were connected as a network, and such may be the fact. In any case the ectodermal system reacts like a network capable of transmission in all directions. There is no evidence for the one-way transmission so characteristic of the nerve cells in higher animals (*cf.* p. 71). There is some evidence that the scattered nerve cells of the endoderm function like a network, but there is scant evidence that the nerve cells of ectoderm and endoderm have connections with each other through the supporting lamella. This apparent lack of connection agrees with the fact that the reactions of the longi-

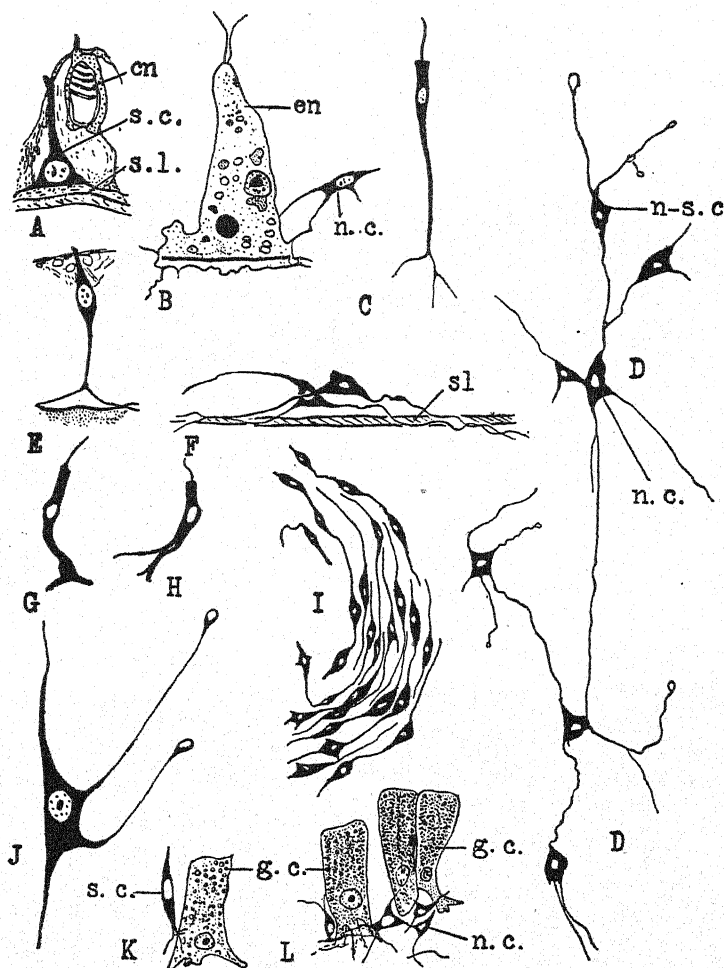


FIG. 218. Nerve cells of *Hydra*, as shown by maceration. A, sensory cell (s. c.) from ectoderm of tentacle, shown in its relation to the supporting lamella (s. l.) and a enidoblast (cn). B, nerve cell of endoderm (n. c.), connected with large endoderm cell (en). C, sensory cell of endoderm. D, network composed of nerve cells (n. c.) and a neuro-sensory cell (n-s. c.) from ectoderm of body (cf. Figs. 216 and 217). E, sensory cell ectoderm of hypostome. F, two nerve cells with processes parallel to the supporting lamella (sl); the processes do not pass through the lamella, although they seemed to do so in this macerated material. G and H, sensory cells from ectoderm of body. I, part of the ring of nerve cells in ectoderm of the foot (cf. Fig. 216). J, neuro-sensory cell from ectoderm of body. K, sensory cell (s. c.) and gland cell (g. c.) of foot. L, nerve cells (n. c.) and gland cells (g. c.) of foot.

(From J. Hadzi, 1909, *Arbeiten zoologischen Institut Wien*, vol. 17.)

tudinal musculature are active and coördinated, whereas those of the circular musculature are sluggish, as though transmission were from cell to cell as in the neuroid transmission of sponges (*cf.* p. 308).

The hydra, accordingly, exhibits in its ectoderm the cellular mechanism for the type of nervous coördination that is typical for cœlenterates. Sensory cells, or *receptors*, receive stimuli, as a result of which impulses are established and transmitted by the nerve cells to the muscle processes, or *effectors*, where the reaction occurs. If the gland cells of the foot are under nervous control, as they may be, they also are effectors comparable with the muscle processes. In addition to these effectors, which are dependent upon the nerve cells for stimuli, there are the cnidoblasts, which are called *independent effectors* since they appear to react independently of the sensory-neural mechanism. In hydras, there is no localization of nerve cells except ringlike collections in the foot and hypostome (Figs. 217 and 218). The processes of the nerve cells tend to run lengthwise on the tentacles and perhaps on the body, although the exact arrangement is difficult to ascertain. In cœlenterates such as jellyfishes, which are more active forms than the hydra, localization of nerve cells and their processes appears in well-defined nerve rings containing many cells with similar orientation. Such localizations may be regarded as first steps in the formation of a central nervous system.

If we recall the definition of irritability as the capacity as the result of which protoplasm responds to stimuli or changes in its environment, it is apparent that the foundation of behavior in the hydra, as in a vertebrate or a protozoan, is the irritability of protoplasm. All the cells of the hydra have the capacity of irritability, but those of the sensory-neuro-muscular mechanism are specialized in this regard. Although experiments like those which have demonstrated the nervous functions of larger animals cannot be performed with an animal as small as the hydra, the functions of certain cells can be inferred from their relationships and our knowledge concerning the reactions of similar cells in other animals. Reception of stimuli and establishment of nervous impulses by the sensory cells, transmission and discharge of impulses by the nerve cells, and the resultant action of effectors occur in the hydra.

If a "system" is defined as a "group of organs" performing some general function, the hydra has no nervous system, although one often speaks of the "nervous system" in hydra. In general, the nervous mechanism of cœlenterates is a *receptor-effector* system, in contrast with the effectors alone which occur in sponges, and the *receptor-adjustor-*

effector systems of higher animals. Further comparisons of the mechanism of coördination in animals will be undertaken after the nervous system of the earthworm has been described, since the organization of this mechanism in annelids is intermediate between what is found in coelenterates and in vertebrates.

Reproduction and Development. At certain seasons of the year, particularly in the fall, hydras reproduce by *syngamy* or the union of

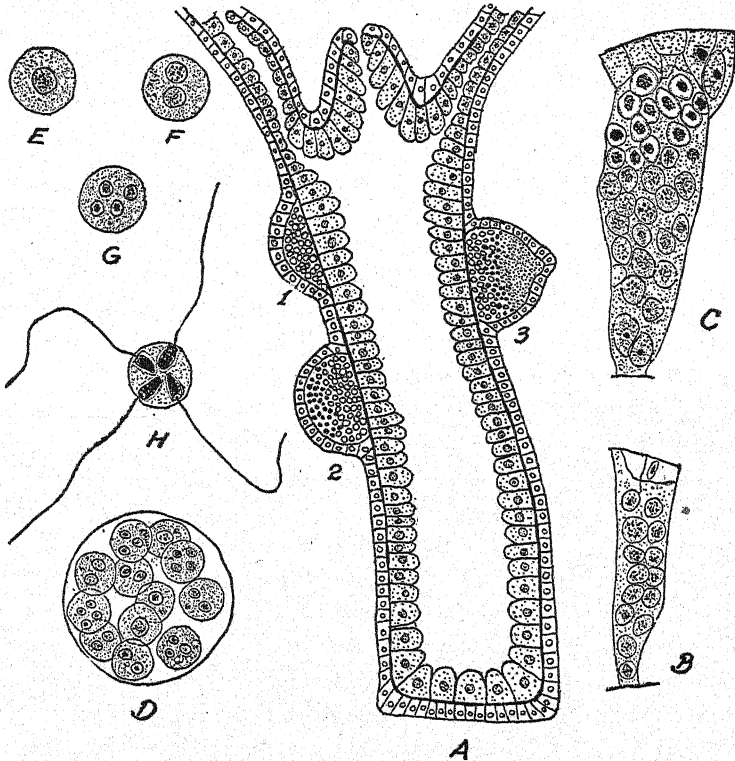


FIG. 219. Differentiation of the male germ cells in *Hydra*. A, diagrammatic longitudinal section, showing successive stages (1, 2, and 3) in the formation of a testis. B, longitudinal section of a cyst from testis (A-1), showing spermatogonia. C, longitudinal section of a cyst from testis (A-2), in which synapsis is occurring in the distal germ cells. D, cross section of a cyst in which the meiotic divisions of the nuclei of the primary spermatocytes are occurring; cytosomal constrictions do not take place. E, F, and G, isolated cells from a cyst such as that shown at D. H, four spermatozoa formed from the common cytoplasmic mass that has descended from the primary spermatocyte and from the four nuclei that have arisen by the two meiotic divisions.

(B-H from G. W. Tannreuther, 1909, *Biological Bulletin*, vol. 16.)

gametes. The *testes* are usually located on the distal half of the body, the *ovaries* near the middle. Testes may appear first and ovaries later on the same animal, or both may be present together. Animals that thus possess functional ovaries and testes in the same individual are called *monœcious*, or *hermaphroditic*. Although this is the usual condition in hydras, individuals that seemed to be male or female exclusively, and hence *diœcious*, have been reported. There are no sexual characters in hydras except ovaries and testes with their contained *ova* and *spermatozoa*. Both ova and spermatozoa arise usually from interstitial cells (Figs. 219 and 220). When the spermatozoa are fully matured, they may be seen moving actively within the testis. They are discharged by the periodic opening of the apex of the testis, which thus liberates successive swarms. The spermatozoön then swims about until it dies or comes in contact with an ovum that has become exposed by rupture of its covering of ectoderm (Fig. 220, C 1). When a spermatozoön unites with an ovum, a zygote is formed, undergoes cell division, and secretes a shell-like cyst about itself. Development proceeds within the cyst until an outer layer of cells, the ectoderm, and a solid inner mass, the endoderm, are formed (Fig. 220 C). The cyst becomes detached from the parent and drops to the bottom at a stage of development which differs in the various species of hydras. Tentacles eventually develop, and the embryo breaks from its cyst, attaches itself, develops an enteron, forms a mouth, and so becomes a miniature hydra (Fig. 220 D). When the zygote is formed in late fall, the developing individual passes the winter within the cyst.

Hydras frequently produce new individuals by *budding*, which is sometimes referred to as asexual reproduction. It is, essentially, reproduction by cell division. There is first an accumulation of nutrient material in the endoderm cells at some place toward the middle of the body, and cells in the ectoderm of this region divide repeatedly to form a budlike swelling. An extension of the enteron grows into the bud, which then appears as a blind outgrowth of the two layers of the body wall (Fig. 211). Tentacles appear as outpushings of ectoderm and endoderm, and finally the mouth is formed. If food is abundant, the bud may remain attached to the parent for some time and in extreme cases may rebud to form several generations in a branching system. Usually, however, the connection between parent and offspring is constricted, and the bud is detached as an independent individual soon after the tentacles and mouth become functional.

Regeneration. Like many other cœlenterates, hydras have extensive powers of regeneration. When a hydra is cut transversely into two

pieces, a new basal part appears on the piece having tentacles and new tentacles on the basal piece. In a few days two complete hydras will have been formed and will have gradually assumed the normal proportions. If fed they will grow to full-sized individuals in the same manner as a bud after detachment. Similar regeneration and subsequent growth may occur even when the hydra is cut into several pieces.

The Hydroids and Hydromedusæ. With a few exceptions the hydroids are marine animals. They are usually attached in at least

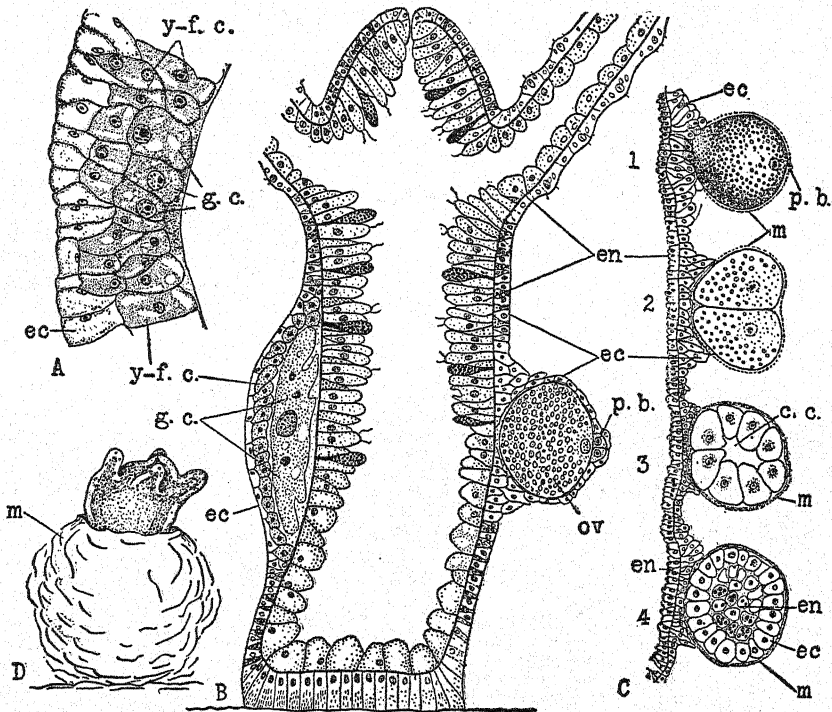


FIG. 220. Development of *Hydra*. A, section of ectoderm (*ec*) showing an early stage of the ovary with several oöcytes (*g. c.*) surrounded by yolk-forming cells (*y-f. c.*). B, longitudinal section showing, on the left, a late stage in growth of the oöcyte (*g. c.*) and, on the right, an ovum (*ov*) and polar bodies (*p. b.*) covered by a layer of ectodermal cells (*ec*). This layer ruptures shortly after meiosis, leaving the egg, as seen in C 1, surrounded by a delicate membrane (*m*), which becomes a heavy cyst as development progresses. The polar bodies (*p. b.*) break loose from the egg and disintegrate in the water. C, stages in development: 1, fertilized egg; 2, two-cell stage; 3, blastula, showing cleavage cavity (*c. c.*); 4, gastrula, showing ectoderm (*ec*) and endoderm (*en*). D, young *Hydra*, escaping from cyst (*m*).

(A and C, from G. W. Tannreuther, 1908, Biological Bulletin, vol. 14.)

one phase of their life-cycle, and most species form colonies of many individuals which are variously specialized in correlation with feeding,

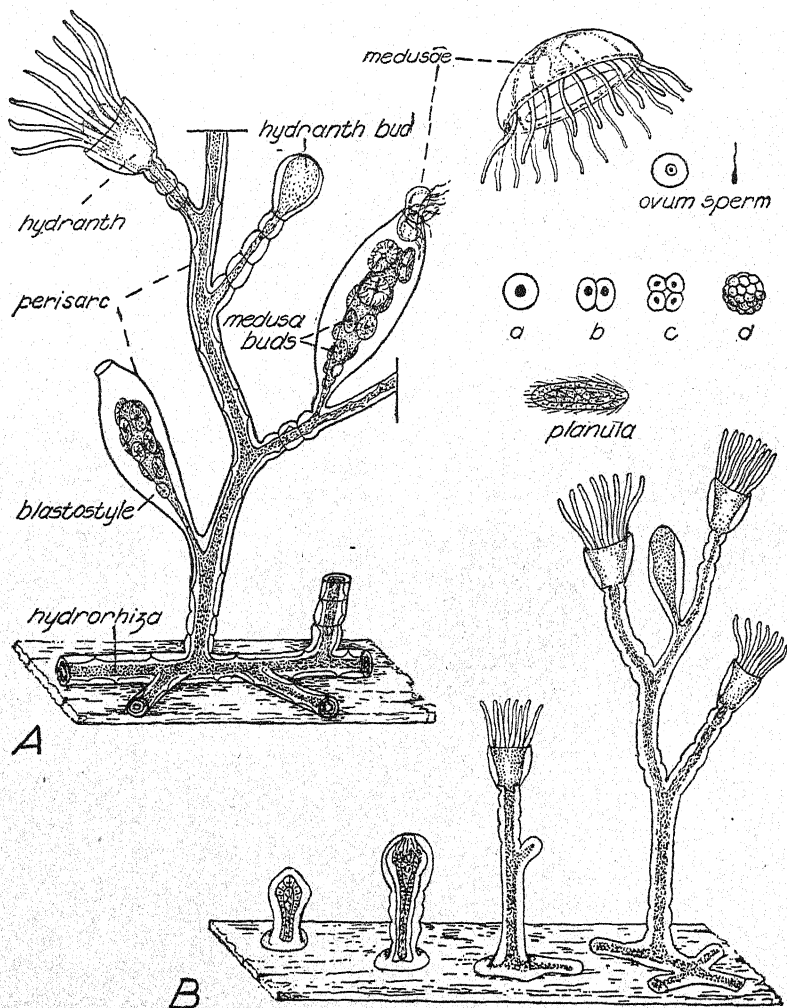


FIG. 221. Life-cycle of *Obelia*, showing alternation of generations. *A*, portion of a colony. *B*, development of a colony after attachment of the planula. *a*, zygote; *b*, two-cell stage; *c*, four-cell stage; *d*, blastula.

protection, and reproduction. The life-cycle in some species includes a jellyfish stage or hydromedusa. The species *Obelia geniculata* is representative. In its hydroid phase or generation, this species of *Obelia* is a colony which may contain thousands of individuals, or

polyps, each comparable with a single hydra and united as all the buds of a hydra would be if they did not become detached. The obelia colony in fact begins as a single polyp, which grows and buds until it consists of many upright stems bearing polyps and arising from the rootlike *hydrorhiza* that has grown along the surface of attachment (Fig. 221 B). In the fully developed colony there are three types of individuals (Fig. 221 A): (1) *hydranths*, which have mouths and tentacles and are the feeding polyps; (2) *blastostyles*, which are modified polyps that have neither mouths nor tentacles and that produce the medusæ; (3) *medusæ*, or jellyfishes, which arise as buds upon the blastostyles, are liberated, and grow to sexual maturity as free-swimming individuals.

The obelia colony, with its three types of individuals, thus arises by the process of budding. The medusæ, or jellyfishes, which constitute one of the types of buds thus formed, are specialized for swimming and become detached from the colony. When these medusæ reach maturity, they are males and females having either *testes* or *ovaries*. The *ova* and *spermatozoa* are discharged into the water, where they unite to form *zygotes* at the time of fertilization. The zygote develops to a ciliated free-swimming stage, the *planula*, which settles to the bottom, becomes attached, and develops into a polyp, from which a new colony is formed. After producing its medusæ, the colony dies; and after producing its ova or spermatozoa, the medusa dies. Thus one may say that there are two generations which alternate: the hydroid generation, reproducing by budding; and the medusa generation, reproducing by syngamy. The term alternation of generations, or *metagenesis*, is applied to such life-cycles. The medusæ formed by hydroid colonies and other medusæ of this sort are called hydromedusæ to distinguish them

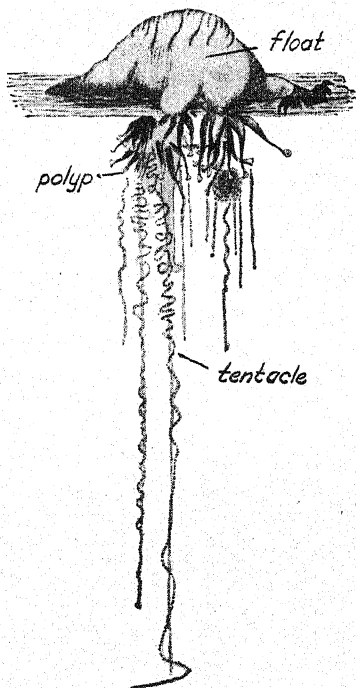


FIG. 222. The "Portuguese man-of-war," *Physalia*, floating at surface of the ocean.

(From T. J. and W. A. Haswell, "Textbook of zoölogy," copyright, 1921, by The Macmillan Co., reprinted by permission.)

from the jellyfishes included in the Class Scyphozoa, which are scyphomedusæ.

Not all genera of the Hydrozoa exhibit alternation of generations. In such forms as *Hydra* and *Clava*, there is a polyp but no medusa; others, such as *Gonionemus*, have a medusa, but the hydroid stage is represented only by a limited amount of budding. The jellyfish *Liriope* has only the medusa, since the *zygotes* develop without any suggestion of a hydroid stage.

Other Hydrozoa. Related to the hydroids and the hydromedusæ are the hydroid corals, or *Hydrocorallinæ*. They have a massive skeleton of carbonate of lime, which somewhat resembles the skeleton in the true corals. The extinct forms represented by the fossils called *Graptolites* probably belong to the Hydrozoa. Another type is the *Siphonophora*, of which the "Portuguese man-of-war," *Physalia*, is an example (Fig. 222). *Physalia* is a colony of specialized individuals having a gas-filled float that supports the whole. The tentacles are laden with nematocysts, which can affect the human skin as severely as the stinging of many wasps. These tentacles capture such prey as small fishes and crustaceans, which are then drawn up to the feeding polyps near the float. There are also medusalike individuals which are not liberated but produce the ova and spermatozoa.

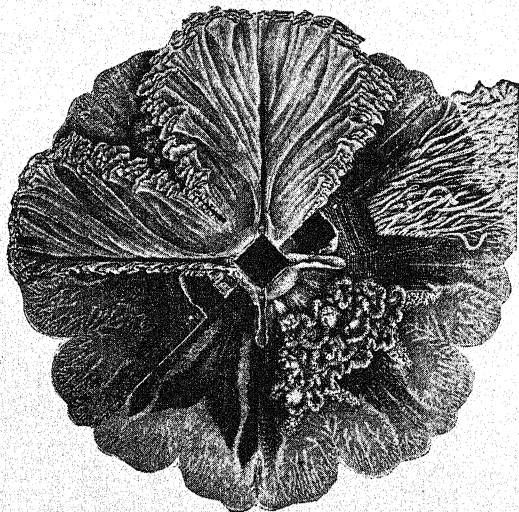


FIG. 223. The scyphozoan jellyfish, *Cyanea artica*; oral view, partially dissected (cf. Fig. 224).

(From L. Agassiz, "Contributions to the natural History of the United States of America," 1860, Little, Brown and Co.)

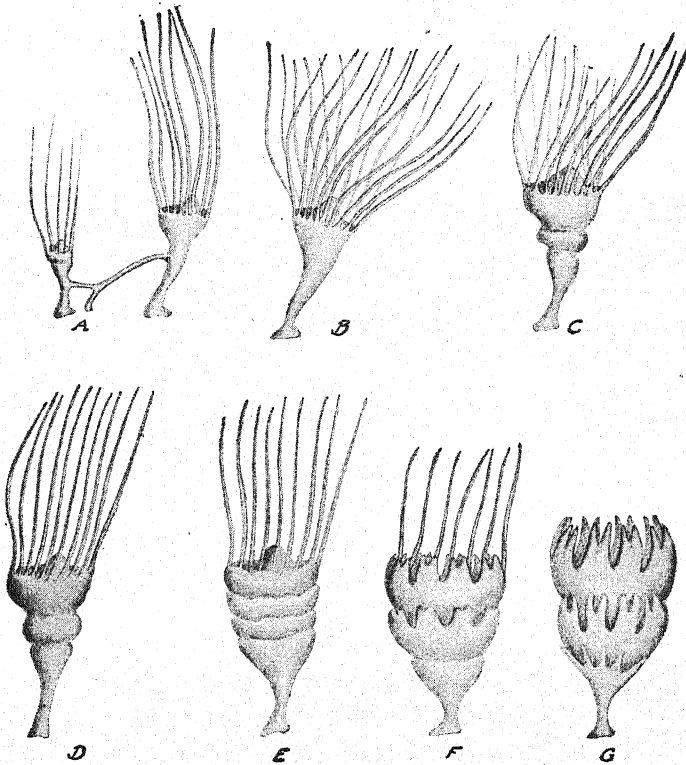


FIG. 224. Life-cycle of a scyphomedusan, *Cyanea arctica*. A, reproduction of polyps by budding. B, polyp, or scyphistoma. C-G, formation, by fission (cf. p. 353), of the ephyrae, which give rise to adult jellyfish (cf. Fig. 223).

(After C. W. and G. T. Hargitt, 1910, Jour. Morphology, vol. 21.)

The Class Scyphozoa

Most of the jellyfishes called hydromedusæ are small like *Gonionemus*. The jellyfishes known as scyphomedusæ, which comprise the Class Scyphozoa, are mostly of larger size (cf. Fig. 138 b and C, p. 219). There is a record of a *Cyanea arctica* 12 feet in diameter and with tentacles over 100 feet in length (Fig. 223). However, the amount of solid material in such an individual would be small, because jellyfishes are composed principally of water. The Genera *Cyanea*, *Dactylometra*, and *Aurelia* are representative Scyphozoa found in North Atlantic waters. In typical cases the life-cycle of a scyphozoan consists of an attached polyp generation from which a free-swimming jellyfish generation arises by the transverse budding, or strobilization, of saucer-like individuals, the ephyrae, that become detached and grow into the adult jellyfishes (Fig. 224).

The Class Anthozoa

The Anthozoa are represented by the familiar sea-anemone, *Metridium dianthus* (Fig. 225), of the New England Coast, and by the true corals, such as *Astrangia danæ* and the many species that abound in tropical seas (Fig. 227). These corals are like small sea-anemones to which a skeleton of carbonate of lime might be added as a secretion from the ectoderm and which might have budded to form colonies with many individuals. The part played by corals in the formation of coral islands and the coral limestone of various formations has given these cœlenterates an important rôle in geologic history.

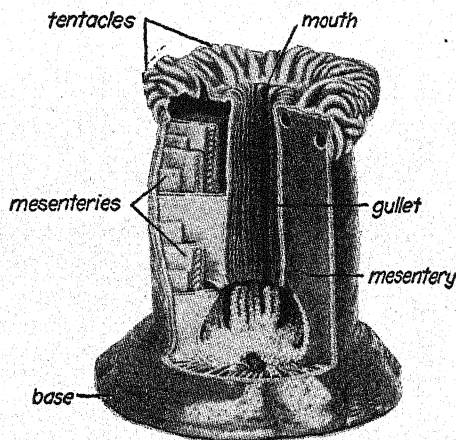


FIG. 225. A representative anthozoan, *Metridium dianthus*.

(From photograph of a Jewell model, courtesy of F. M. Jewell, Carlinville, Ill.)

The Cœlenterate Body-plan

In the simplest cœlenterates the body is like a sac having a wall composed of two layers, the ectoderm and endoderm, and hence called diploblastic. The single opening of this sac, which is called the mouth, although it functions as both mouth and anus, is surrounded by tentacles. The radial symmetry characteristic of the phylum is obvious in most species. In the more specialized cœlenterates there is a middle region, which may have several kinds of cells and may then be termed a mesodermal layer. Such cœlenterates are more properly called triploblastic than diploblastic animals. As compared with sponges, the cœlenterates are evidently animals of more complex type. As compared with vertebrates, however, they are very lowly animals. They have,

nevertheless, important features in common with all the higher phyla. If comparisons are made between cell layers, the ectoderm of the cœlenterate is comparable with the epidermal layer of the skin, and the

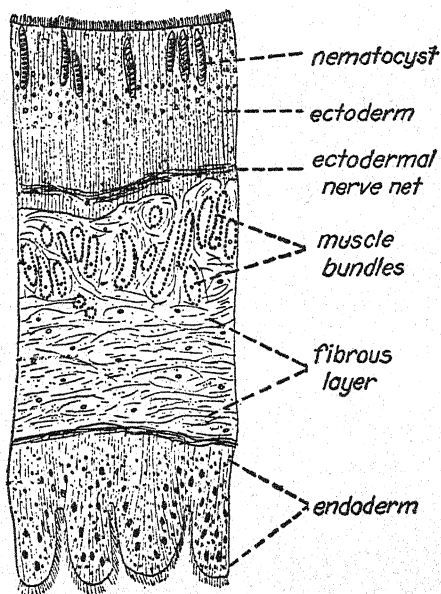


FIG. 226. Cellular structure of a sea anemone, from transverse section of a tentacle.

(After L. H. Hyman, "The invertebrates: Protozoa through Ctenophora," copyright, 1940, by McGraw-Hill Book Co., printed by permission.)

endoderm with the mucous membrane of the digestive tract in a vertebrate. The parts of the body derived from what is called mesoderm in such forms as vertebrates are absent, except in so far as the middle region found in some cœlenterates may be considered the beginning of a mesodermal layer. A comparison between the adult cœlenterate and the gastrula stage in the development of higher animals is deferred until the closing paragraphs of this chapter.

The Phylum Ctenophora

The *Ctenophora*, which are commonly known as sea-walnuts or comb-jellies, are animals with a biradial symmetry, ectodermal and endodermal layers like those of the Cœlenterata, a mesodermal region, and eight meridional rows of swimming plates formed by fusion of cilia. The phylum includes the Class *Tentaculata*, which have tentacles, and

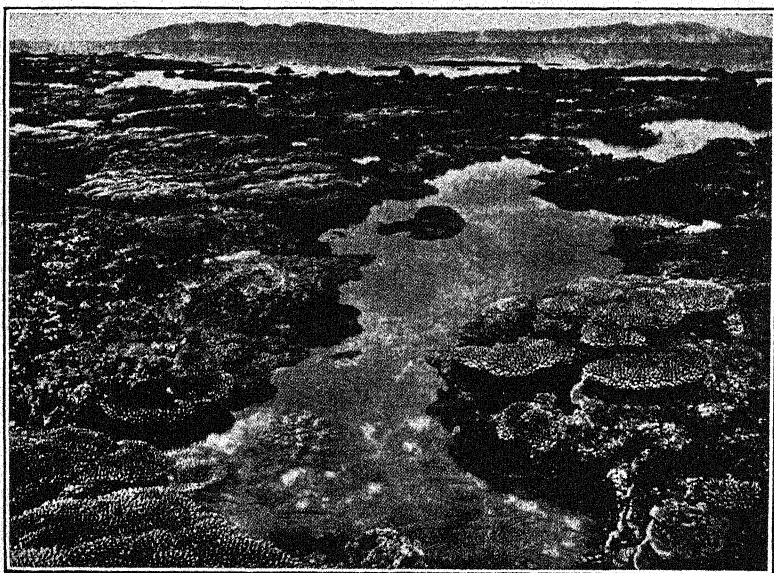
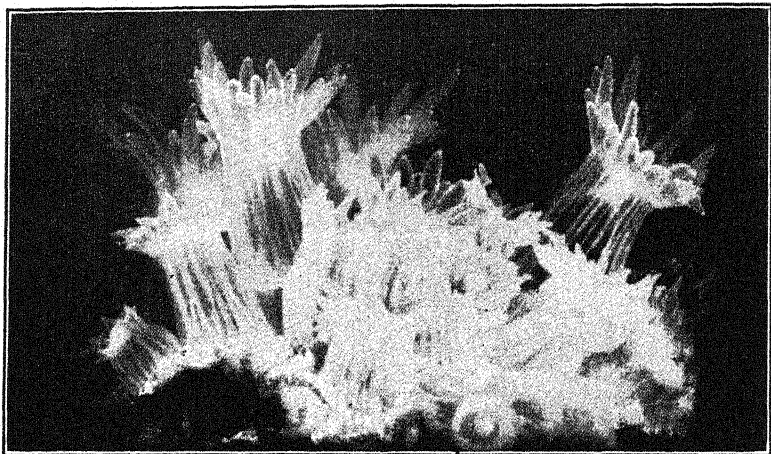


FIG. 227. Coral polyps and a coral reef. *Above*, a colony of *Astrangia dance*, the only species found as far north as Cape Cod on our Atlantic Coast. The polyps have a skeleton of carbonate of lime similar to that seen in dried specimens of corals. The tentacles and radially symmetrical body are characteristic features of these coelenterates, as of *Hydra*. *Below*, the Great Barrier Reef of Australia, showing prolific coral growths exposed at low tide. In the middle distance the lagoon separating the reef from the distant shore can be seen. This great reef extends for more than 1200 miles along the Australian coast. (*Above*, from life. *Below*, after W. Saville Kent. Both photographs by courtesy of the American Museum of Natural History.)

the Class *Nuda*, which are "nude" in the sense that they are devoid of tentacles. Ctenophores are small marine animals that float and swim near the surface, although a few species have become adapted to creeping upon the bottom. The free-swimming forms are sometimes present in countless numbers and thus may constitute a very important element of the floating life of the ocean (Fig. 228). Their

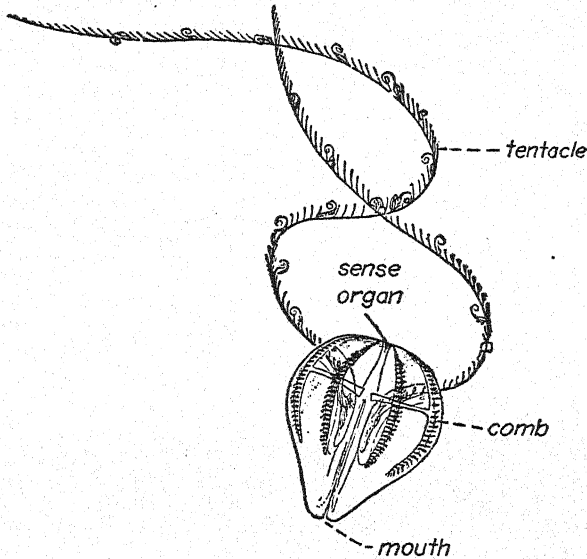


FIG. 228. A representative ctenophore, *Hormiphora plumosa*, as it swims in the ocean.

(After C. Chun, "Die Ctenophoren des Golfes von Neapel," 1880.)

food consists of whatever small animals they may capture with the aid of their tentacles or with the parts related to the mouth in species not possessing tentacles. Unlike the coelenterates, they have no nematocysts, but the Tentaculata have adhesive cells which hold fast to the prey until it can be drawn to the mouth. The species without tentacles feed upon smaller and weaker prey, which they capture in a variety of ways. It has been stated that the ctenophores can be classified in a single phylum with the coelenterates and that this classification is used by many zoölogists. Yet it has long been recognized that the resemblances between coelenterates and ctenophores are very general. The ctenophores lack the nematocysts, which are so unique a feature of coelenterates, and they have a body-plan which is quite distinctive.

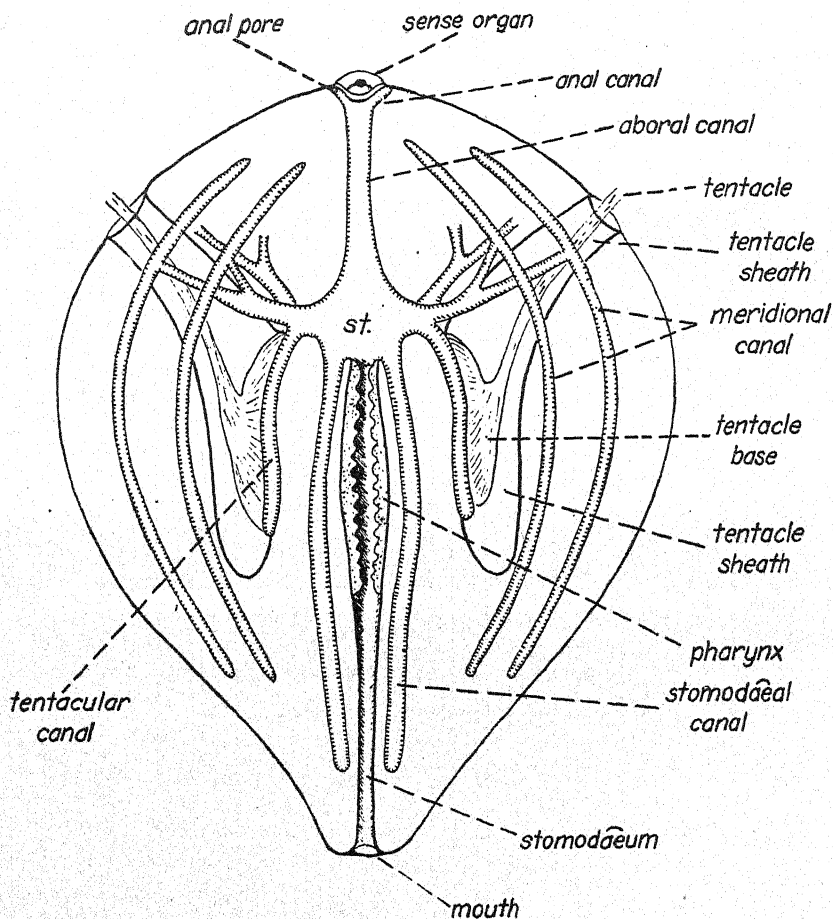


FIG. 229. Structure of a ctenophore; diagrammatic. *st.*, stomach.

(After L. H. Hyman, "The invertebrates: Protozoa through Ctenophora," copyright, 1940, by McGraw-Hill Book Co., printed by permission.)

As will appear from Figure 229, the structure of a ctenophore is rather complicated for an animal whose basic organization is so simple. The eight rows of combs, located in eight meridional planes, are a unique feature of this phylum. Each row consists of a series of comb-like plates which are composed of fused cilia. It is this feature which has given the phylum its name Ctenophora, meaning "comb bearers." All ctenophores have these rows of combs, except that the rows may have been lost or modified in some specialized members of the phylum. Locomotion is effected by the rhythmical beating of the combs, which

has been much studied as an example of ciliary action controlled by a nervous system. There are no fossil records of ctenophores, unless certain markings like those left by jellyfishes can be so interpreted (*cf.* p. 312).

Representative Types. Common and representative genera to be found along our North Atlantic Coast are *Pleurobrachia*, a tentacle-bearing type, and *Mnemiopsis*, which is without tentacles. A very specialized type is the Genus *Cestus*, the "Venus' girdle" of the Mediterranean (Fig. 138 A, p. 219), in which the body is compressed laterally and elongated to form a thin plate, sometimes as long as 4 feet, which is a gigantic size for a ctenophore. The minute, creeping ctenophores, *Cæloplana* and *Ctenoplana*, represent another extreme type. When these two genera were discovered, they were hailed as representing an evolutionary transition from the radial and attached coelenterates to the bilateral and creeping flatworms. Further study has shown that *Cæloplana* and *Ctenoplana* are merely very much specialized ctenophores, and not forms that suggest a step in the evolutionary origin of the simplest bilateral animals.

Because ctenophores are well-nigh impossible to preserve for satisfactory examination in the laboratory, they must be studied alive at the seashore. Hence, many students do not have an opportunity to become well acquainted with these remarkable animals. They are a fascinating type of life when one has the opportunity to know them. For the purposes of an introductory study they can be sufficiently described by these brief comments and by the figures, particularly Figure 229.

Body-plans in Cœlenterata, Ctenophora, and Higher Metazoa

Despite their differences the cœlenterates and ctenophores exhibit the same basic type of structure, namely, a saclike body with a single opening, the mouth-anus, and a single internal cavity, the enteron or digestive cavity. The wall of this sac is two-layered in the simplest cœlenterates, but in the more specialized cœlenterates and in all the ctenophores there is also a middle region, which can be fairly called mesodermal. Thus, ectoderm, endoderm, and a primitive mesoderm are found in these animals. The basic symmetry is radial, but this has become biradial in many cœlenterates and in all ctenophores. Because they have these features in common to set them apart from the higher Metazoa, the cœlenterates and ctenophores may be placed in a group, the Radiata, standing apart from the Group Bilateria, which includes the higher Metazoa (Fig. 135, p. 215). When such a classifica-

tion is interpreted in terms of evolution, the cœlenterates and ctenophores must be regarded as a very ancient type of animal life. True, they show great specialization along their own lines, but they have a simple and primitive body-plan, namely, a two-layered structure with a single opening to a digestive cavity. It may be significant from the standpoint of evolution that such a body-plan occurs as a transitional stage, the so-called gastrula stage, in the development of many higher animals (*cf.* Figs. 81 G and H, 283 B, and 340 G, pp. 138, 394, and 459).

CHAPTER 11

THE FLATWORMS: PLATYHELMINTHES AND NEMERTINEA

The name "flatworm" is applied to members of the Phylum *Platyhelminthes* and the Phylum *Nemertinea* because most of these animals are wormlike and flattened dorso-ventrally. They are thus contrasted with the "roundworms" and with the "segmented worms," which are described in later chapters. The nemertineans are frequently classified within the Phylum *Platyhelminthes* as a Class *Nemertinea*, instead of being given the rank of a phylum. In contrast to the Mesozoa, the Porifera, and the Cœlenterata, the flatworms are bilaterally symmetrical animals. They have, therefore, antero-posterior differentiation; in other words, they have "head" and "tail" ends and they go head-end first like most familiar animals. They have also dorso-ventral differentiation, as seen in the vertebrates with their "back" and "belly" surfaces.

The Phylum *Platyhelminthes*

The members of the Phylum *Platyhelminthes*, meaning "flatworms," may be characterized as animals with an anterior or head end and the bilateral symmetry characteristic of such antero-posterior differentiation, with dorso-ventral differentiation, with a digestive cavity or enteron having a single opening, the mouth, with ectoderm, endoderm, and mesoderm, but without a body cavity of any sort, with an excretory system of flame bulbs and ducts, called protonephria, and with complex reproductive organs of a distinctive type. The phylum includes three classes: the Class *Turbellaria*, or planarians and other free-living flatworms; the Class *Trematoda*, or flukes; and the Class *Cestoda*, or tapeworms. Although the turbellarians are the most representative of the *Platyhelminthes*, they are not familiar animals like the parasitic flukes and tapeworms, which are widely known at least by name.

Most *Turbellaria* are small and inconspicuous animals. They live in the shallow waters of the ocean and in fresh water; some tropical

species live on land, but only in humid places. A few turbellarians are parasitic upon the outer surfaces of other animals. Since the Trematoda and the Cestoda are much specialized as parasites, it is necessary to use the Turbellaria alone in making comparisons between the flatworms and other phyla. When the Turbellaria are thus used to represent the Platyhelminthes, the members of this phylum are seen to exhibit certain primitive features, such as the single opening to the digestive tract, and also more specialized features, such as their bilateral symmetry. They are in fact the simplest type among the *Bilateria* or bilateral Metazoa (cf. Fig. 135, p. 215). The Trematoda and Cestoda are important because they present excellent examples of the structural modifications characteristic of parasites and because they include many parasites dangerous to man and to domesticated animals.

The Class Turbellaria

There are three principal orders in the Class Turbellaria, the *Polycladida*, *Rhabdocaelida*, and *Tricladida*, distinguished by the form of their digestive systems (Figs. 230, 231, and 232). The polyclads are exclusively marine; the rhabdocœles and triclads occur mostly in fresh water. The body is usually flattened in the manner characteristic of

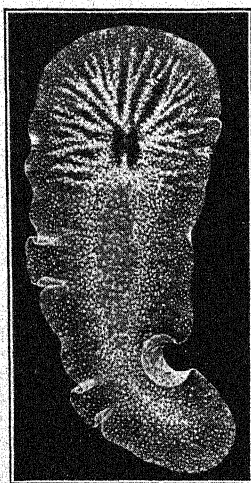


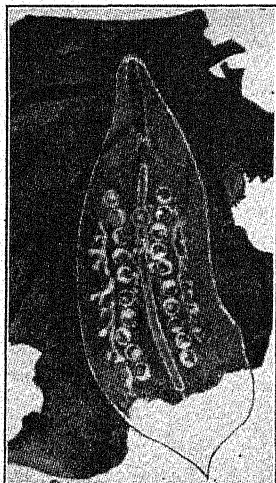
FIG. 230. A polyclad, *Leptoplana pallida*.

(From A. Lang, "Die Polycladen des Golfes von Neapel," 1884.)



FIG. 231. A triclad, *Dendrocoelum lacteum* (left); and a rhabdocœle, *Mesostoma ehrenbergi* (right).

(From P. Steinmann and E. Bresslau, "Die Strudelwürmer," 1913.)



the phylum and always differentiated anteriorly into a region called the head. Although cilia are found upon the entire external surface of some turbellarians, they usually occur in restricted areas. The name Turbellaria, from "turbella," small whirlpool, refers to the effect produced by the action of these cilia (Fig. 237). The mouth may be located in any position along the ventral midline from the anterior to the

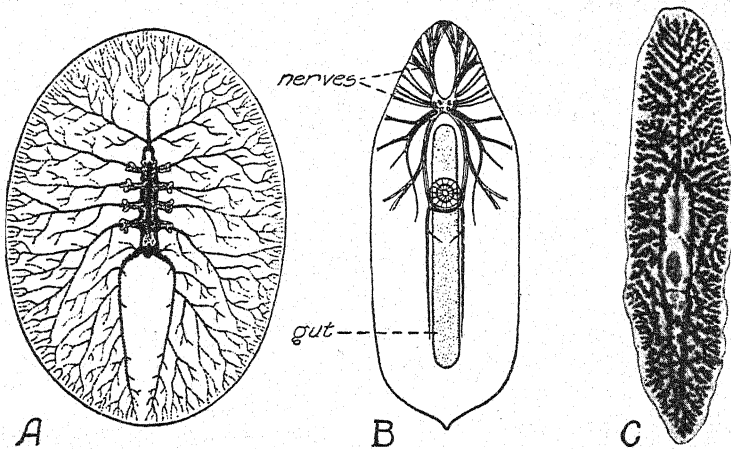


FIG. 232. Digestive system in representative turbellarians. *A*, a polyclad, *Planocera*, with many branches to the gut. *B*, a rhabdocoele, *Mesostoma*, with a rodlike gut cavity; the nervous system is also shown. *C*, a triclad, *Dendrocoelum*, in which the gut has three main divisions, one anterior and two posterior, and many lesser branches. *A* and *B*, diagrammatic; *C*, from photograph of preserved specimen.

(From E. Bresslau in W. Kükenthal, "Handbuch der Zoölogie.")

posterior end in different species, although the usual, and apparently the primitive, position is near the center of the body. A schematic representation of the internal structure shows an ectodermal epithelium covering the body and an endodermal epithelium lining an enteron (Fig. 233). Between these epithelial layers is a mesodermal region, known as the parenchyma, composed of a network of mesenchyme cells in which are distributed muscle cells, gland cells, and certain free cells, and in which the excretory, nervous, and reproductive systems are embedded. The turbellarian is thus triploblastic, or three-layered, in contrast with such a coelenterate as the hydra, which is diploblastic (cf. Fig. 211, p. 316).

Fresh-water Planarians: Habitat, General Structure, and Activities. The term planarian is sometimes applied to both the polyclads and tri-

clads, although it more commonly refers to the triclads alone. Such triclad planarians are common in fresh water. Like the hydras, they are well-known animals, suited to illustrate the structures and functions occurring in the phylum of which they are members. The species *Planaria maculata*, *P. agilis*, and *P. dorotocephala* are widely distributed in North America. They occur in ponds and streams, where they are usually found on the shaded sides of submerged objects. As they thus avoid strong light, they are probably nocturnal in many of

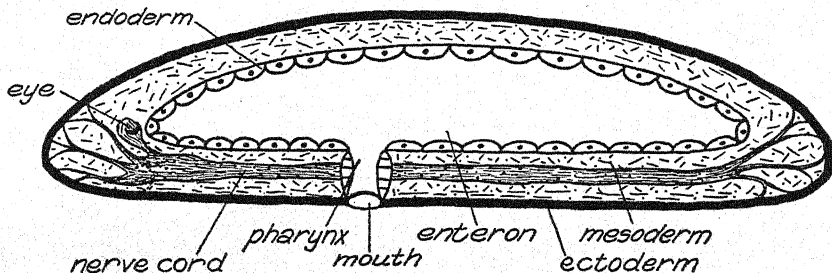


FIG. 233. A flatworm, in longitudinal section; diagrammatic.

their activities. In nature they feed upon the bottom ooze with its microscopic plants and animals, upon dead animals, and upon living animals such as small mollusks and arthropods, which are captured by enfolding the prey and then applying the extended pharynx (Fig. 234). When bits of meat are placed in a dish containing planarians that have not been fed recently, the worms begin to move about, and soon most of the individuals will be found with the pharynx attached



FIG. 234. Lateral view of a planarian feeding upon a nemertinean (shown in cross section at *x*). *a* and *b*, successive positions of the worm.

(From R. Pearl, 1903, *Quarterly Jour. Microscopical Science*, vol. 46.)

to the food (Fig. 235). They can be collected in nature by this method, and, if the meat is placed in flowing water, they may be seen crawling from beneath the stones and heading upstream toward the bait. Species of the Genera *Dendrocoelum* and *Procotyla* have a special organ at the anterior end by means of which they seize active prey and convey it to the pharynx, which is protruded from the mouth to complete the capture. The primary means of locomotion is by the cilia of the ventral and lateral surfaces, which beat in mucus secreted as the

animal moves (Fig. 238). The worms also perform a great variety of muscular movements in response to various stimuli, as may be seen when they move about upon a surface covered with gravel or other obstacles.

Structures and Functions Related to Metabolism. In feeding, the tubelike pharynx is extended from the mouth and attached to the food, which may be partially digested by fluid from the pharynx before it is

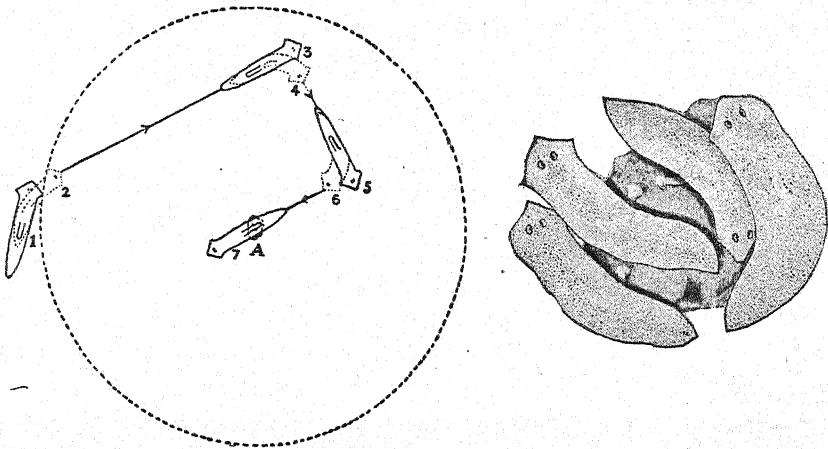


FIG. 235. Feeding in planarians. *Left*, reactions of a planarian to food: *A*, the food; 1-7, successive positions taken by the worm after entering a diffusion area (circle) of food juices. *Right*, planarians with pharynges extended as they feed upon a bit of meat.

(*Left*, from R. Pearl, *op. cit.*; *Right*, drawn by George T. Kline.)

transferred to the enteron. The relationships between mouth, pharynx, and enteron appear in a median longitudinal section (Fig. 239). What is called the *mouth* is the external opening of a sheathlike cavity which surrounds the *pharynx* and is partially obliterated when the pharynx is protruded. The opening at the free end of the pharynx leads into the tubular cavity within this organ, which in turn leads into the *enteron* with its three main branches and lesser subdivisions (Fig. 232 C). Digestion occurs in this enteron, or gut cavity, and also, within certain of the cells lining the gut in a manner comparable with intracellular digestion in hydras. The digestive system thus constituted assumes in part the function of a circulatory system, since it extends to all parts of the body and so distributes the digested food. The products of digestion, as well as the oxygen absorbed through the ectodermal epithelium, are also distributed by way of the fluid-filled

spaces in the parenchyma. Thus, the materials necessary for assimilation and the subsequent dissimilation of the protoplasm reach the cells.

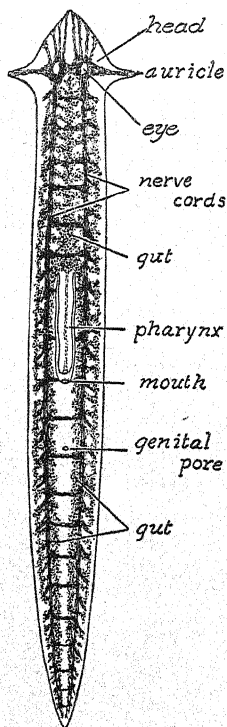


FIG. 236. *Planaria dorocephala*, showing nervous and digestive systems; diagrammatic.

(Slightly modified from C. M. Child, "Senescence and rejuvenescence," copyright, 1915, University of Chicago Press, printed by permission.)

tion, and the system may be called excretory.

The Nervous System and Irritability. The nervous system is well developed in correlation with the complex musculature of planarians. (Fig. 236). Beneath the eyes is a concentration of nervous tissue, the

The *excretory system*, as it is usually called, consists of minute tubules beginning as *flame bulbs* in all parts of the mesodermal region and uniting to form larger tubes which have a number of external openings (Fig. 240). The flame bulbs, also called flame cells, are so named because they have flickering tufts of cilia. The tubular cavities in which these cilia are located are intracellular spaces within one or more cells and are continued as intracellular ducts within the cells that make up the tubules. In some of the larger tubules the cavities may be intercellular. Such a system is a distinctive feature of trematodes and cestodes as well as turbellarians. It is apparently universal among flatworms, although very difficult to recognize except in non-pigmented species, where it can be studied in the living animal. The name *protonephridia* is applied to organs thus composed of flame bulbs and ducts leading to external openings. In ascribing an excretory function to this system, it is supposed

that the tufts of cilia in the flame cells and any other cilia in the tubules set up a current that flows toward the external openings. If water enters such a system from the surrounding tissues, it presumably contains excretions in solu-

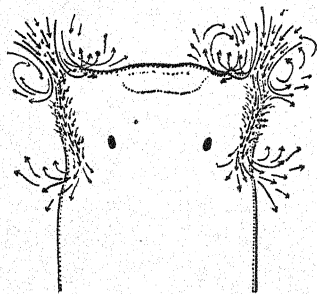


FIG. 237. Anterior end of *Dendrocoelum*, showing water currents due to ciliary action in region of the auricles; diagrammatic.

(From E. Bresslau in W. Kükenthal, "Handbuch der Zoologie.")

so-called *brain*; two *nerve cords* extend to the posterior end of the body; and there are transverse connections throughout the length of these cords. The brain and nerve cords with their cross connections thus constitute what may be called a *central nervous system*. From the brain and cords strands of fibers, which may be called *nerves*, extend to all parts of the body, particularly to the anterior end. The *nerve cells*, or neurons, are not easily recognizable in planarians, but they can be demonstrated in certain regions (Fig. 241), and it is presumed that the relationship of sensory, motor, and perhaps adjustor

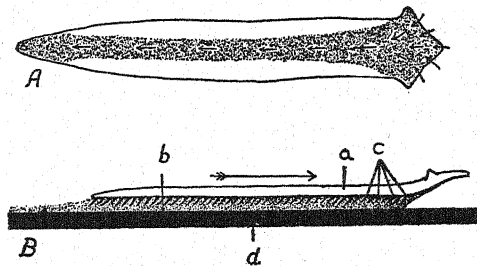


FIG. 238. Locomotion in planarians. *A*, ventral surface of animal showing distribution of cilia; arrows indicate direction of ciliary currents. *B*, mechanism of gliding movement; *a*, planarian seen from side; *b*, layer of mucus (thickness exaggerated) secreted by animal; *c*, cilia (exaggerated); *d*, substrate; the arrow indicates the direction in which the organism is moving.

(From R. Pearl, 1903, *Quarterly Jour. Microscopical Science*, vol. 46.)

cells is comparable with that of other invertebrates (*cf.* Fig. 337, p. 456) which have central nervous systems. A similar central nervous system is found in other turbellarians (*cf.* Fig. 232 B). Evidently, these animals have a well-organized nervous mechanism as the basis for their complex sensory and muscular reactions. Sections through the anterior masses and the nerve cords show what are regarded as *nerve cells* lying at the periphery and enclosing a central region of fibers which are supposed to be the processes of these nerve cells or other cells belonging to the system. The structure of the *eye* in many planarians (Fig. 242) indicates that light from a definite direction may be an effective stimulus as well as mere illumination, although there seems to be no mechanism for image formation. Planarians respond to a variety of stimuli with a rather high degree of coordination.

The Reproductive System, Reproduction, and Development. The reproductive system is highly developed (Fig. 239). The worms are hermaphroditic; that is, each individual has both male and female

organs. The male system includes *testes*, in which the spermatozoa arise, and the *ductus efferentes* (vasa efferentia), which join the paired

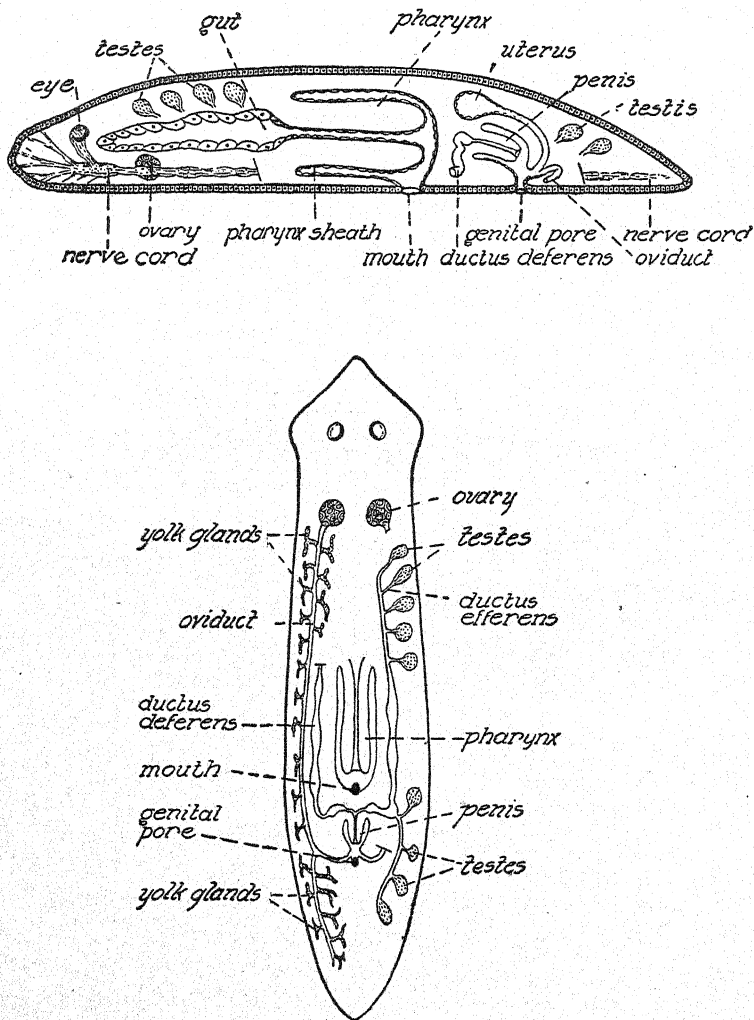


FIG. 239. Reproductive organs of a planarian; diagrammatic. Above, in lateral view. Below, in ventral view.

ductus deferentes (vasa deferentia). These become enlarged posteriorly into *seminal vesicles*, where the spermatozoa are stored in advance of copulation. The *penis*, or copulatory organ, where the seminal vesicles unite in a common duct, lies in a cavity called the *genital atrium*, which opens externally by the *genital pore* posterior to the

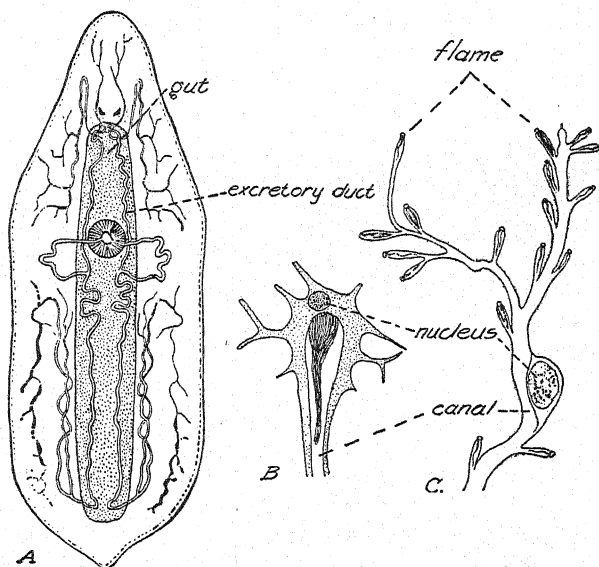


FIG. 240. Excretory system of turbellarians. A, the principal canals of the rhabdocœle, *Mesostoma ehrenbergi*. B, flame bulb formed by a single cell, as in planarians. C, multiple flames within the branches of a single cell, as in *Mesostoma*.

(From E. Bresslau in W. Kükenthal, "Handbuch der Zoölogie.")

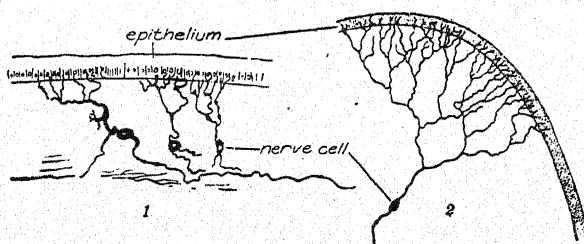


FIG. 241. Nerve cells in turbellarians. 1, multipolar nerve cells of *Planaria alpina*, with free endings in the epithelium and a branch to muscle fibres; 2, bipolar nerve cell of *Bdelloura candida*, with free endings in the epithelium.

(From E. Bresslau in W. Kükenthal, "Handbuch der Zoölogie.")

mouth. The relationship of the penis to this cavity resembles that of the pharynx to its sheath, and during copulation the penis is thrust from the genital pore in the same manner as the pharynx from the mouth during feeding. The female system includes a pair of *ovaries*,

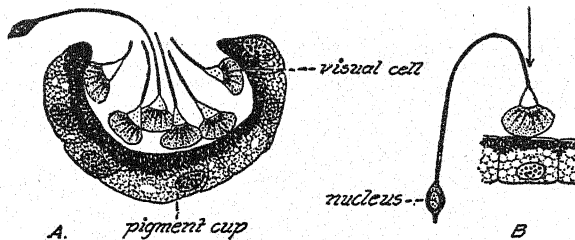


FIG. 242. Eye of a planarian. *A*, transverse section, showing pigment cup containing visual cells (some omitted); the nuclei of the visual cells lie outside the pigment cup. The dorsal surface of the planarian would be toward the top of the page (*cf.* Fig. 239 Above). *B*, single visual cell and the bordering region of the pigment cup; the visual cell would be stimulated by such light rays as come in the general direction shown by the arrow.

(From W. H. Taliaferro, 1920, *Jour. Experimental Zoölogy*, vol. 31.)

in which the ova arise, and *oviducts* which extend posteriorly to unite as a common duct that enters the genital atrium. Opening into each oviduct throughout its length are the so-called *yolk glands*, which are

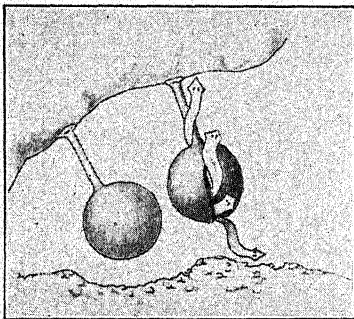


FIG. 243. Planarian egg-capsules and the young hatching.

(Drawn by George T. Kline.)

masses composed of *yolk cells* that pass into the oviducts. A glandular organ of problematic function, sometimes called the *uterus*, may communicate with the genital atrium. Other accessory parts are found associated with the genital atrium in some species of planarians. Planarians have been observed to copulate, with an apparent exchange of spermatozoa, but this does not exclude the possibility of self-fertilization. Spermatozoa may be found along the oviduct and collected at its anterior end, so that fertilization presumably occurs at some place in

this duct. At the time of egg-laying, fertilized ova, or *zygotes*, and great numbers of yolk cells are found in the atrium. Several zygotes surrounded by many thousands of yolk cells become enclosed in a capsulelike *shell* secreted by the atrial region, and the "egg" thus

formed is laid attached by a stalk to the submerged objects on which the worms are found (Fig. 243). Within these egg capsules the zygotes develop, using the yolk cells as food, until they hatch as juvenile worms able to begin life upon the bottom after the manner of their parents. Reproduction by *syngamy*, or the fusion of gametes, is thus followed by development.

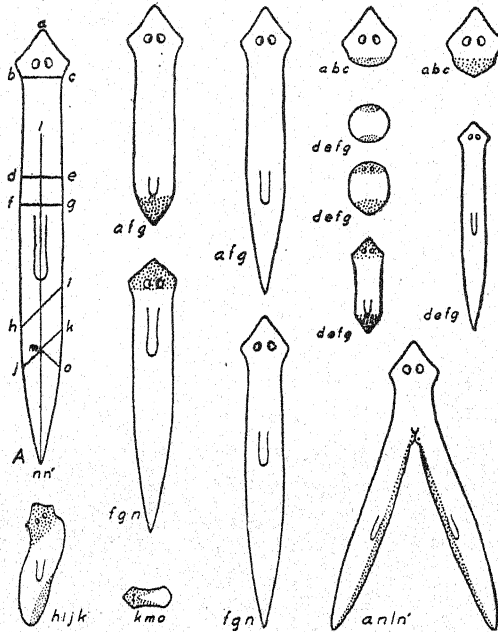


FIG. 244. Regeneration in planarians. The regeneration of pieces, cut from a worm along the lines in A, is shown by labelling of the remaining figures. For example, a piece removed by cuts along lines *de* and *fg* regenerates as shown by the figures marked *defg*. Stippled areas represent portions formed from scar-tissue that appears during the early stages of regeneration.

In many species of planarians reproduction also occurs by *transverse fission*, usually in the post-pharyngeal region. In most of these species the worm merely constricts and so divides itself into a head- and a tail-piece, each of which heals the wound, forms the missing parts by cell division, localization, and differentiation, and undergoes regulation of proportions. If this method of reproduction is compared to budding in hydra, it is seen that in hydra numerous cell divisions and localizations of cells occur before the bud separates from the parent, whereas in the planarian a part is separated and then becomes a new individual as a result of cell division and localization in the region of

fission. The process of strobilization in the scyphomedusæ can be compared with fission in planarians, since the ephyrae are formed by constriction and complete their differentiation into medusæ after detachment (cf. Fig. 224, p. 335).

Regeneration. Many species of planarians have great powers of regeneration, as may be shown by a variety of experiments (Fig. 244). The regenerative process by which a piece of the animal thus forms a perfect individual involves healing of the wound surfaces, formation

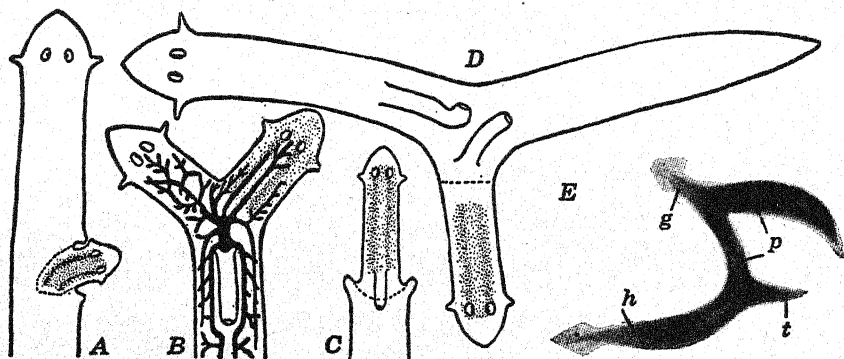


FIG. 245. Grafting in planarians. *Euplanaria tigrina novangliæ* (stippled) grafted into *Euplanaria dorotocephala*: A, at 14 days after implantation; B, at 42 days; C, graft united to posterior end of host, 14 days after implantation; D, graft united to host by its posterior surface. E, *Euplanaria dorotocephala* (g) grafted into *E. tigrina novangliæ* (h): two pharynges (p) and a tail (t) have been induced.

(From J. A. Miller, Jr., 1938, "Physiological Zoölogy," vol. 11.)

of a small amount of new tissue at these regions as a result of division, localization, and differentiation, apparently of *totipotent* or *formative cells* (cf. pp. 302 and 460), and regulatory changes by which the piece gradually assumes normal proportions. It may then grow to a full-sized worm. In this process, even the small and irregular fragments exhibit a polarity such that the axes of the original body are preserved in the new individual; and each piece has the capacity to form a normal adult, except in the special cases of *heteromorphosis*, in which an abnormal planarian is formed, for example, an individual with two heads or two tails instead of one.

Grafting. The plasticity of the planarian organization is further illustrated by experiments in grafting (Fig. 245). Pieces from different individuals or even from different species, if made to adhere, may grow together and so produce compound individuals that may

live for considerable periods. Similarly, grafts can be made in some species of hydroids; and in the reassociation of cells in sponges (p. 309) it has been possible to unite the dissociated cells of two species in a common mass which lives for a time. In all these cases the identity of the tissue is not lost if two species are involved. It would be interesting to learn what would happen if such composite individuals could be kept alive and should reproduce sexually. In plants where the

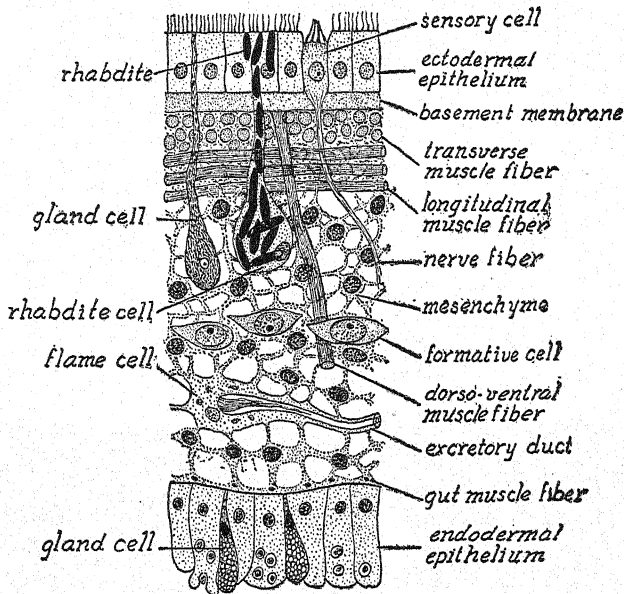


FIG. 246. Cellular structure of a planarian, as seen in a longitudinal section; diagrammatic.

acceptance of grafts from other species is not uncommon, the graft may live indefinitely upon the "stock" without change of its genetic nature. For example, "scions" of the standard varieties of apple are commonly grafted on crab-apple stocks to produce the apple trees sold by nurseries for planting. In such cases the scion, not the stock, determines the nature of the subsequent growth and reproduction. There is no theoretical reason for thinking the process would be different in an animal, but it would be interesting to find out.

Cellular Structure and Functions. The epidermis, or outer layer of epithelium, which is derived from the ectoderm of an earlier stage, is ciliated only in certain regions in adult planarians. The cuboidal or flattened cells rest upon a thick basement membrane, which functions as an elastic skeleton (Fig. 246). Attached to the inner face of

this membrane is a *musculature* of longitudinal, transverse, and diagonal fibers, and dorso-ventral fibers extend from this region to the basal membrane of the opposite side. A syncytium of mesenchymatous tissue, the *parenchyma*, occupies the central portion of the body, filling the space between the digestive and reproductive organs. Within this

syncytium are embedded the *gland cells*, which form the mucous secretions and the bodies called *rhabdites*. In the meshes of the syncytium are also found the *formative cells*, which give rise to the gametes and to the new parts formed during regeneration. The muscle fibers are cytoplasmic extensions of cells whose nuclei are inconspicuous. The lining of the enteron is derived from the endoderm during development and is composed of cells that carry on intracellular digestion, like the endoderm cells of hydras (cf. p. 322), and of gland cells, which apparently produce digestive juices. The central nervous system, which lies ventrally upon the muscle fibers, consists of *nerve cells* and their outgrowths, which are the *nerve fibers*.

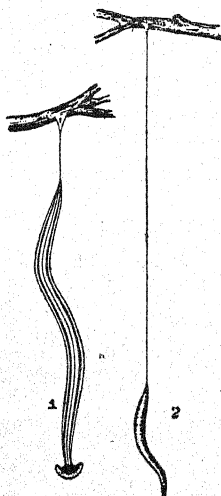


FIG. 247. Land planarians lowering themselves by threads of mucus. 1, *Bipalium kewense*; 2, *Rhynchodemus terrestris*.

(From E. Bresslau in W. Kükenthal, "Handbuch der Zoölogie.")

Other Turbellaria. The fresh-water planarians are representative of the Order *Tricladida*, so called because the gut has three principal subdivisions (Fig. 232 C). The marine triclads are much like those of fresh water. The so-called land planarians are large triclads that live in the upper layers of the soil or upon vegetation growing in a warm and moist atmosphere, like that of the tropical regions in which they are found (Fig. 247). In temperate climates they

sometimes occur in greenhouses, into which they have been introduced, presumably from the tropics.

The turbellarians included in the Order *Rhabdocœlida* are so named because the gut is rod-shaped (Figs. 232 B and 240 A). Most rhabdocœles are of small size and hence not so favorable for study as planarians, although abundant in fresh water. Some have the mouth and pharynx in the center of the ventral surface, as in *Mesostoma* (Fig. 232 B), but in most species the mouth occupies an anterior position. In these rhabdocœles which have the mouth near the anterior end, the brain lies dorsally, and from it the two principal nerve cords extend posteriorly in the ventral part of the body. Including the transverse

connections between the ventral nerve cords (*cf.* Fig. 236), the make-up and position of the nervous system in these forms are like those of the nervous system in other invertebrate animals, namely, a dorsal brain, circumpharyngeal connectives, and a pair of ventral nerve cords, which may be separate or fused (*cf.* Fig. 350, p. 476). Some rhabdocœles have marked powers of reproduction by fission and so form chains of individuals which remain together for a considerable time before they separate.

In the Order *Polycladida* the gut is many-branched and the body much flattened (Fig. 232 A). In the simpler polyclads the mouth is central, and the pharynx is a funnel-like structure that can be protruded from the mouth to enclose the food. The polyclads are exclusively marine, in contrast with the rhabdocœles, which are typically fresh-water species, and the triclads, which occur in both salt and fresh water. This order does not include many species, and the individuals are seldom numerous, although they abound in some localities, for example, the Gulf of Naples.

The Class Trematoda

The Class Trematoda includes the worms known as flukes. All trematodes are parasitic, although they are not so greatly modified in relation to parasitism as the cestodes. In most flukes the body is covered by a cuticle instead of an epithelium, and there is usually a sucker encircling the mouth and another upon the ventral surface. However, the flattened body is characteristic of the Platyhelminthes, and the internal structure, which includes a gut, shows the same general relationship of parts that is found in Turbellaria. The Trematoda are divided into the Orders *Monogenetica* and *Digenetica*, according to their parasitic habits and the related modifications of structure and life-cycle.

Monogenetica. The monogenetic trematodes are external parasites upon the outer surfaces of aquatic animals, mostly vertebrates, or in cavities near the surface, such as the mouth and the urinary bladder (Figs. 248 and 249). Monogenetic parasites do not alternate between host species in the course of the life-cycle. In correlation with their attachment in relatively exposed positions, such trematodes have well-developed adhesive *suckers* and sometimes *hooks*. The mouth lies anteriorly. The gut is usually divided into right and left branches as in *Polystoma*, although it may be single, as in *Aspidogaster* (Fig. 248). The nervous system is especially developed in the region of the adhesive sucker, as well as anteriorly (Fig. 249 E). The animals are her-

maphroditic, and their reproductive organs are comparable with those in turbellarians. The "eggs," which consist of a single *zygote* and a number of *yolk cells* surrounded by a *shell*, as in planarians, are laid free in the water or are loosely attached to the host. The *ciliated larva*, which hatches from the egg, swims about until it finds a host or dies. The development is simple as compared with that of digenetic trematodes.

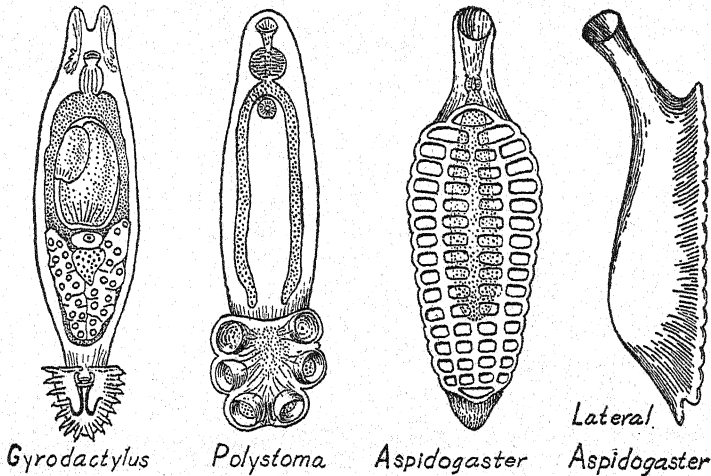


FIG. 248. Monogenetic trematodes. *Gyrodactylus* is parasitic upon the outer surface and the gills of many fresh-water fishes. *Polystoma* is found in the mouth cavity of turtles. *Aspidogaster* occurs in the pericardial and renal cavities of certain mollusks.

Digenetica. The digenetic trematodes are internal parasites having at least two species of hosts in the course of the life-cycle. In the adult stage such trematodes occur almost exclusively in vertebrate animals, usually infesting either the blood or the digestive tract and its appended parts, the lungs, liver, and urinary bladder. Each species has its particular habitat within its host. In their developmental stages these trematodes are parasitic in snails and sometimes within a second invertebrate host. The adhesive sucker is poorly developed in such species as the lung and liver flukes but well developed in those inhabiting the cavities of the intestines or the bladder, from which the parasite might otherwise be discharged (*cf. Pneumonocæces* and *Diplodiscus*, Fig. 250). The gut is typically divided into two main branches. The nervous system is well organized only in connection with the suckers. The animals are hermaphroditic, and their reproductive organs are comparable with those of turbellarians and of monogenetic trematodes.

A characteristic feature of the group is the life-cycle, which is one of the most complex in the Animal Kingdom. The classical example is the liver fluke of sheep, *Fasciola hepatica*.

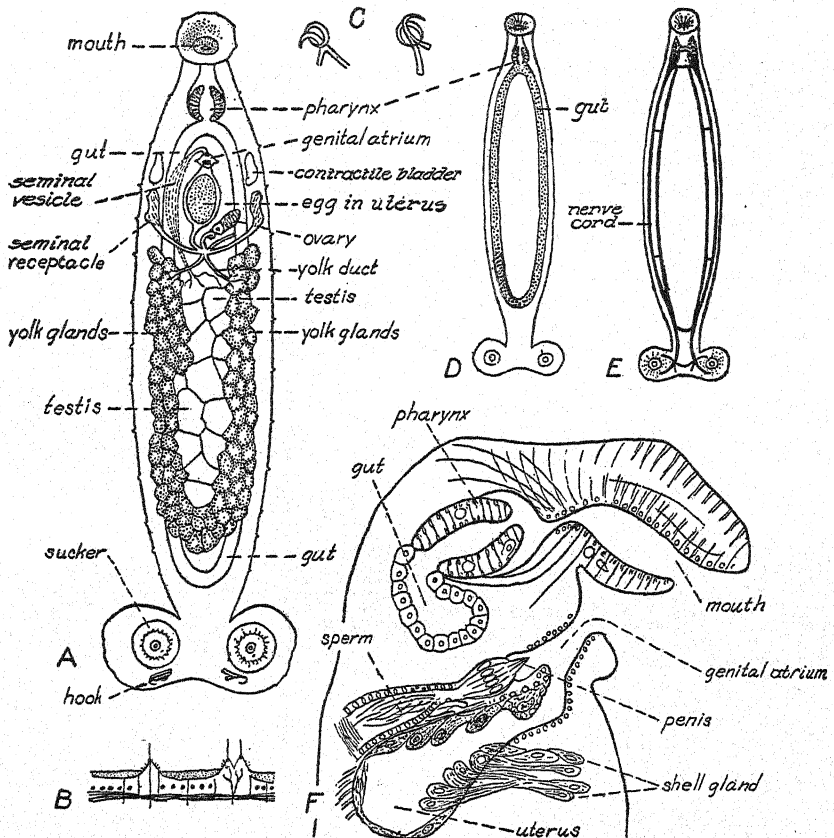


FIG. 249. *Sphyrnura osleri*, a monogenetic trematode parasitic upon the outer surface of the amphibian, *Necturus*. A, ventral view to show internal structure. B, section of surface membrane, with tactile structures. C, small hooks, which occur lateral to the suckers and are surrounded by chitinous rings at the point of projection from the surface membrane. D, digestive system. E, nervous system. F, median, longitudinal section of anterior end.

(Redrawn from R. R. Wright and A. B. Macallum, 1887, *Jour. of Morphology*, vol. 1.)

The adult *Fasciola* is found in the livers of sheep and goats (Fig. 251). It lays "eggs," each of which consists of a *zygote* surrounded by *yolk cells* and enclosed in a *shell* like the egg of a planarian or a monogenetic fluke. These eggs pass through the bile duct to the intestine

and out with the feces of the host. If such an egg reaches water, a ciliated larva, the *miracidium*, is hatched and swims about until it dies or finds a certain species of pond snail. In the latter event it bores into the snail and develops into a saclike organism, the *sporocyst*, containing ova which develop without fertilization, that is, parthenogenetically, to form a generation called the *redia* I. These *redia*

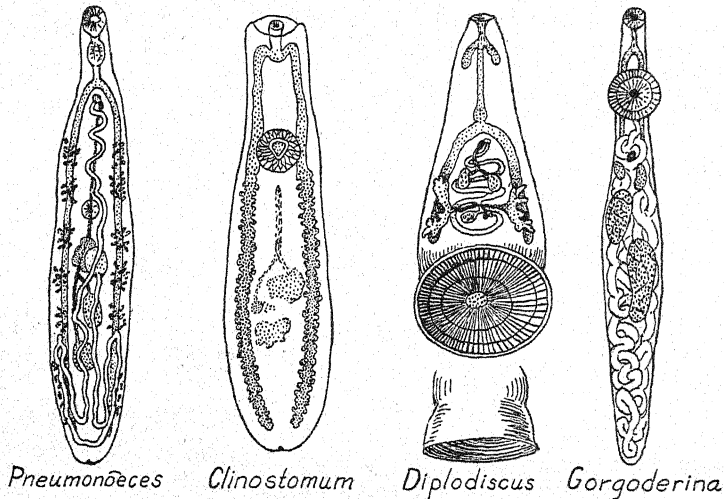


FIG. 250. Digenetic trematodes. *Pneumonodes* is parasitic in the lungs of frogs and toads. The adults of *Clinostomum* are parasitic in the pharynx and esophagus of fish-eating birds; the larval stages occur in frogs and fishes. *Diplodiscus* occurs in the rectum of frogs; the figure shows the sucker from ventral and side views. *Gorgoderina* is parasitic in the urinary bladder of amphibians.

escape by bursting of the sporocyst and may reproduce parthenogenetically another generation of the same sort, called *redia* II, which in turn may produce *redia* III. The next stage in the cycle, known as the *cercaria*, is produced by the final generation of *redia*, whichever one it may be. These *cercaria* are discharged from their parent *redia*, leave the snail, and swim about in the water, from which they may reach the stomach of a sheep or goat that drinks the water thus infected. If the *cercaria* is not transferred to the necessary host, it can become encysted upon vegetation, such as grass growing at the edge of a pond, and so remain alive for a considerable period. When this vegetation is eaten by a sheep or goat, the cyst is digested; the young fluke reaches the host's intestine, makes its way up the bile duct to the liver, and grows to an adult *Fasciola*. Other digenetic trematodes

have similar life-cycles, with vertebrates as hosts for the adult flukes, and snails as hosts of the intermediate generations.

At first glance this trematode life-cycle seems wholly at variance with the life-cycles of other many-celled animals, for example, the egg-tadpole-adult cycle of the frog. But such a cycle can be com-

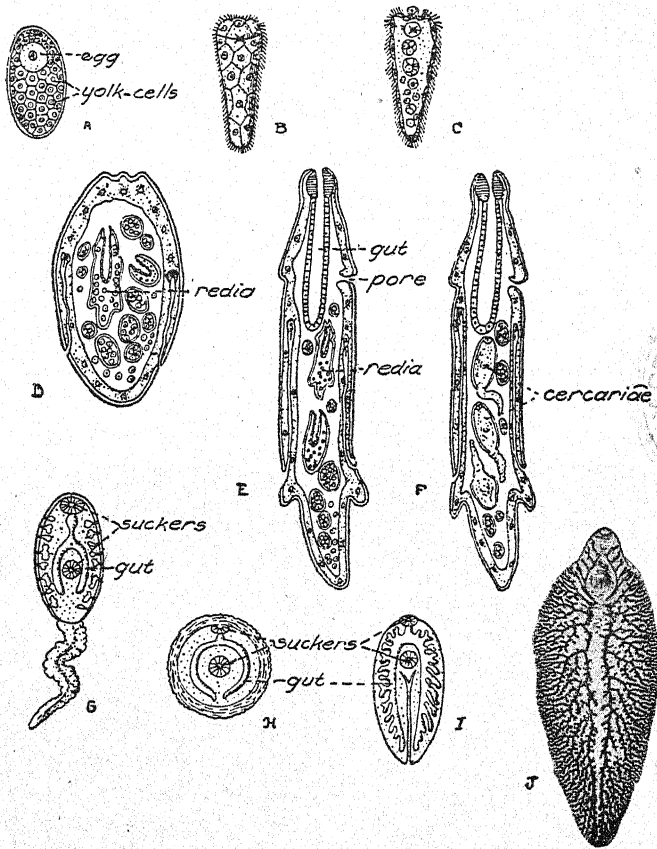


FIG. 251. Life-cycle of the liver fluke, *Fasciola hepatica*. A, egg and yolk-cells within the shell. B, miracidium, or ciliated larva. C, longitudinal section of a miracidium, showing early stages in development of redia. D, sporocyst within which redia are developing parthenogenetically from unfertilized ova; the excretory organs and ducts of the sporocyst are shown in its walls. E, redia, within which daughter redia are developing parthenogenetically; these larvae escape from the parent redia through the pore. F, redia in which cercariae are developing parthenogenetically. G, free-swimming cercaria. H, encysted cercaria. I, young adult. J, mature adult.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

pared with familiar modes of development, if one regards the cycle in trematodes as having arisen by the specialization of a sequence of generations. According to this interpretation, the cycle described for *Fasciola* is equivalent to several generations, only one of which becomes a fully developed fluke. Thus, the sporocysts and rediæ are generations that reproduce precociously by means of parthenogenetic ova, and the cercariæ are early stages in the generation that becomes the mature *Fasciola*. Such a life-cycle may be compared with a cycle involving but one generation for its completion, if the parthenogenetic sporocysts and rediæ are regarded as generations that have been modified by the elimination of later stages in development and by the early appearance of ova that develop without fertilization. The existence of such a life-cycle in trematodes may be regarded as one of the adaptations by which these animals have become adapted to their parasitic life. Parasites must produce a maximum number of offspring and produce them rapidly once the parasite reaches its place in a host. The trematodes meet this necessity of parasitic life in one way, the cestodes in another. The distinctive features in the life-cycle of these trematodes are precocious reproduction, or *pedogenesis*, and suppression of later stages in the generations involved. A few other cases of this sort are known among animals, but none in which the modification is so extreme as in trematodes (*cf.* p. 130).

Certain genera of flukes, such as *Paragonimus*, one of the lung flukes of the Far East, and *Schistosoma*, one of the blood flukes of Egypt, are dangerous human parasites. The United States has no widespread human infections of this sort, although there is always danger that such parasites may be introduced by persons infected in other parts of the world. To establish such a parasite in a new country, however, it would be necessary for its secondary host to become established in the same area, or for the parasite to make use of a local species of snail, as might conceivably happen. Among domestic animals the liver fluke of the sheep was a disastrous pest before its life-cycle became known about 1870. Since that time it has been possible to control the situation by preventing the sheep from drinking infected water or feeding upon vegetation likely to be infected with the encysted cercariæ.

The Class Cestoda

The members of the Class Cestoda are familiar parasites, although infections in man and domestic animals are less common than they were before the life-cycles of tapeworms became known and preventive measures could be taken. A representative tapeworm with its

segments and radially symmetrical organ of attachment has little resemblance to other flatworms, but examination reveals homologies that clearly place these worms with the Trematoda and the Turbellaria. However, the structure of the cestode is more specialized in relation to parasitism than is the structure of the trematode when each is compared with the free-living turbellarians. Not only is the ectodermal layer lacking, as in the majority of trematodes, but the cestode has no digestive tract and no endoderm cells, even in its development. It is the reproductive and excretory systems that establish the relationship, since these parts are unique and fundamentally like those of trematodes and turbellarians. The apparent dissimilarity between the non-segmented fluke or the planarian, on the one hand, and the segmented tapeworm, on the other, is not so important as it might seem, because segmentation does not occur in the Order *Monozoa*; and in the Order *Merozoa* there are some species in which the segments are few in number. The segmentation is in fact only a reduplication of the part of the individual containing the reproductive organs and is not comparable with the segmentation of such a form as the earthworm, which is called metamerism; it may be regarded as a device for increasing the reproductive output.

The Order Monozoa. These non-segmented tapeworms may have an organ of attachment that resembles the headlike scolex of the Merozoa; but they lack the segments, or proglottids, of the Merozoa (*cf.* Figs. 252 and 253), and they have only one set of reproductive organs instead of many sets. Like the Merozoa, they are covered with a cuticle instead of an ectodermal epithelium, and they have no mouth or digestive system with its endodermal epithelium. They have been compared with trematodes minus a digestive tract, and considered a primitive type resembling the ancestors of tapeworms. It is questionable whether they represent such a survival or have arisen by degeneration from the Merozoa.

The Order Merozoa. This order includes the great majority of tapeworms. The individual consists of a *scolex*, which bears organs of attachment, the suckers, and, in many species, hooks, and of a body composed of a varying number of segments called *proglottids*. The adult animal lives in the intestine of its host, attached by its scolex

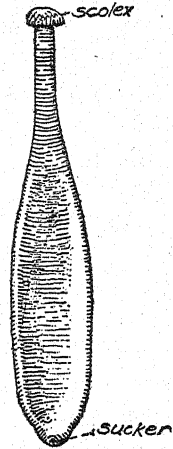


FIG. 252. The monozoan cestode, *Gyrocotyle rugosa*, parasitic in the intestine of a fish.

(From O. Fuhrmann in W. Kükenthal, "Handbuch der Zoölogie.")

and with the chain of proglottids extending into the intestinal cavity. The firm hold of the scolex enables the parasite to maintain its position despite the movement of food along the tract. Adult tapeworms

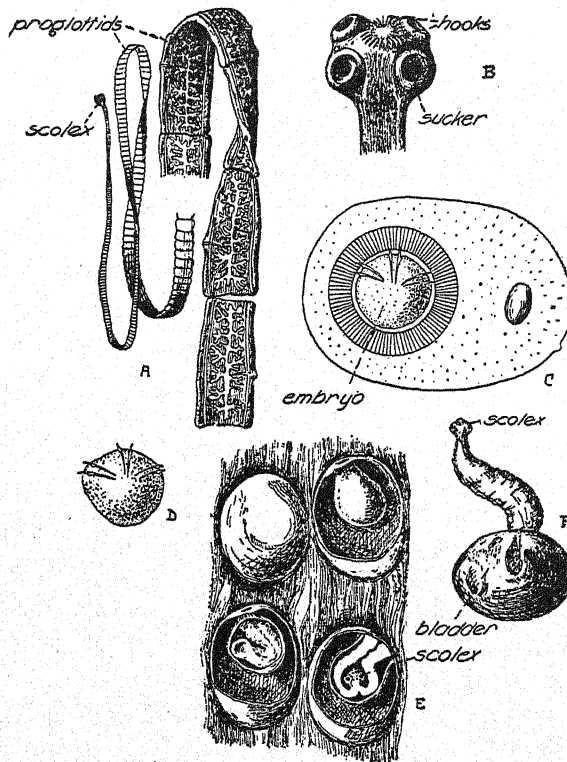


FIG. 253. Life-cycle of the pork tapeworm, *Tænia solium*. A, parts of the worm, showing the youngest proglottids behind the scolex and the oldest (ripe) proglottids at the opposite end. B, scolex of adult tapeworm. C, six-hooked embryo inside its shell and the tough surrounding capsule. D, six-hooked embryo freed from its shell. E, portion of a muscle of the host with bladder worms embedded; successive layers are removed to show internal structures. F, juvenile tapeworm which arises from the bladder-worm by evagination of the scolex.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

vary in size from forms such as *Echinococcus granulosus* (Fig. 255), which is from $\frac{1}{8}$ to $\frac{1}{4}$ inch in length when fully grown, to others such as *Tænia saginata*, which may be 4 to 10 yards in length and have thousands of proglottids. With a very few exceptions all adult tapeworms are intestinal parasites in vertebrate hosts, and their larval

stages are parasites in the bodies of animals upon which the adult host feeds or which are likely to pass into the adult host with its food. The larval host is infected by eggs and embryos from the feces of the adult host. Examples of such host combinations for well-known tapeworms are: man and pig, man and beef cattle, dog and rabbit, dog and flea, dog and sheep, chicken and snail, cat and mouse, and pelican and trout.

The structure and life-cycle of the pig tapeworm, *Tænia solium*, which infests man, is representative (Fig. 253). Infection is still common in countries where raw or imperfectly cooked pork is eaten. The structure is similar to that of *T. saginata*, the beef tapeworm, and that of *T. pisciformis*, which is common in dogs wherever dogs and wild rabbits abound. The scolex bears many hooks and four suckers. Behind the scolex is a budding zone where the proglottids originate. As new ones are formed, the older ones become farther removed from their place of origin and finally become detached, either singly or in short chains, from the free end of the worm to pass out of the host with its feces.

The internal structure of such a tapeworm is relatively simple, except for the reproductive organs (Fig. 254). There is no mouth or digestive system. Food digested and ready for absorption in the host's intestine is apparently absorbed through the surface of the parasite's body. An *excretory system* is present, consisting of flame cells and ducts leading to longitudinal vessels that extend the length of the body. The *nervous system* is little developed except in the scolex, where it is connected with the suckers and hooks. Longitudinal nerve cords extend parallel with the lateral excretory vessels. Sense organs and sensory cells are virtually unknown in such tapeworms, although the animal may respond to stimulation by movements of the scolex and contractions of the body. This degeneration of structures important in free-living animals is common in parasites. The *reproductive system* is complex, and a complete system of male and female organs develops in every proglottid (Fig. 254). In *T. solium* fully differentiated reproductive systems may be seen in the region from the two hundredth to the three hundredth proglottid. Each one of these reproductive systems is comparable with the single set of reproductive organs found in a turbellarian or a trematode. The "egg" likewise consists of a *shell* enclosing a *zygote* and *yolk cells*, although the number of these nutritive cells is not more than four in the eggs of most cestodes. It is probable that self-fertilization occurs, as the copulatory organ may be inserted into the vagina of the proglottid to which it belongs or into the vagina of a neighboring proglottid if the worm is

folded upon itself. Cross-fertilization may occur during similar contacts if two or more worms are living in the same host. As the cells composing the ovaries, testes, and yolk glands in each proglottid are utilized, the eggs thus formed accumulate in the uterus, which grows as the other parts of the system dwindle. Eventually the greater part of the proglottid is occupied by the branching uterus containing tens

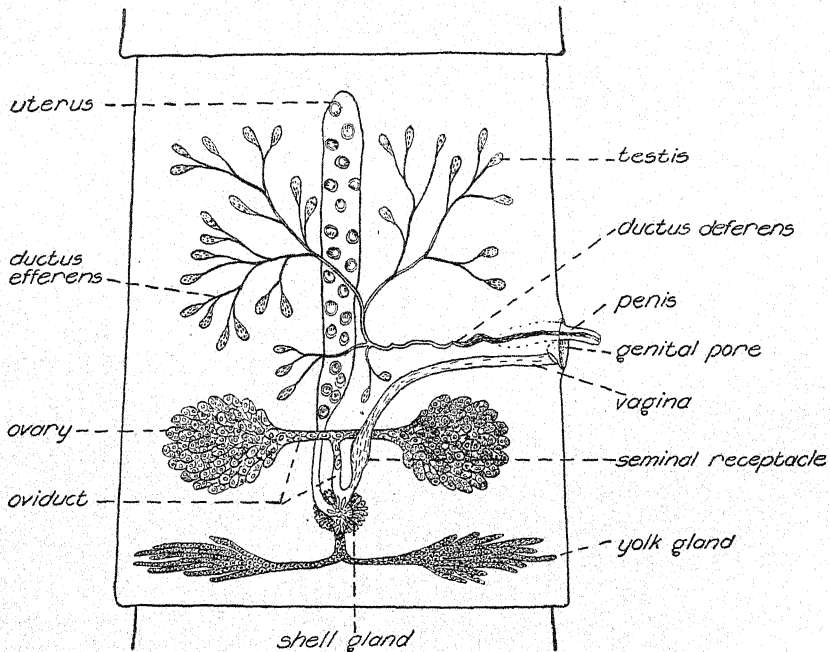


FIG. 254. Reproductive organs of a cestode; diagrammatic.

of thousands of *six-hooked embryos* (Fig. 253 C and D), which have developed from the zygotes. These ripe proglottids become detached, pass out of the host with the feces, and disintegrate. The embryos may thus be liberated on the surface of the ground, where they can survive protected by the shell for months and may be distributed widely like encysted protozoans.

Within the proglottid and the eggshell, development proceeds no farther than the six-hooked embryo unless the egg enters the digestive tract of another host, which is normally the pig if the parasite is *T. solium*. Here the eggshell is digested, but the six-hooked embryo survives and bores its way through the mucous membrane to the blood or lymph vessels. It may then be carried to a place where it develops into what is called the *bladder-worm* because it consists of a bladder

with the scolex and neck of the future adult invaginated from one point on the surface (Fig. 253 E). This bladder-worm cannot develop farther unless it is eaten by the host of the adult, which in this case is man. Once in the human digestive tract, the surrounding flesh of the larval host and the bladder are digested, the scolex is everted (Fig. 253 F), attaches itself to the intestinal wall, begins a rapid formation of proglottids, and so produces the adult worm. Such an adult may

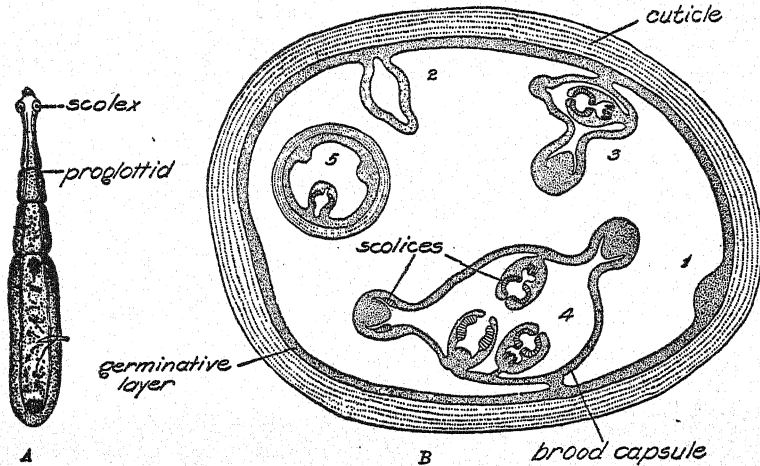


FIG. 255. Life-cycle of the cestode, *Echinococcus granulosus*. A, adult tapeworm. B, hydatid. The wall of the hydatid cyst consists of two layers, an outer cuticular membrane and an inner germinative layer, from which brood capsules arise. Successive stages in the growth of these capsules with the development of a number of scolices are shown at 1, 2, 3, and 4. Sometimes daughter cysts are formed and set free within the original mother cyst, as at 5.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

live some years, forming and detaching thousands of proglottids, each with countless eggs.

A modification of this typical structure and life-cycle is seen in the species *Echinococcus granulosus*, which is found as an adult tapeworm in dogs and as a larva in sheep and sometimes in man (Fig. 255). In the adult there are never more than three or four proglottids, which ripen one at a time, but a large number of individuals may infect the intestine of a single host. This fact is explained by examination of the larval stages corresponding to the bladder-worm. In *Echinococcus* these stages, which are called *hydatids*, are large, cyst-like structures containing many scolices (Fig. 255 B). The presence of even a single hydatid in man or a sheep is much more serious than

any infection with an adult tapeworm. The adult can be removed by purgatives, whereas the hydatid may grow to large dimensions and may prove fatal to its host at an early stage if it develops in such an organ as the brain. Even in the muscles of a limb it cannot be removed with certainty by a surgical operation because of its ramifying growth.

Tapeworm infections are now comparatively rare among adult human beings in communities where sanitary precautions are in practice. Meat inspection, cold storage, and widespread knowledge regarding the mode of infection have almost eliminated infection with *Tænia saginata* and *T. solium* as a serious problem for the United States and

western Europe, as compared with the infections that occurred before the life-cycles of these parasites, and hence the means of preventing them, became known about 1850. The once common human tapeworms may become medical and zoölogical curiosities within the next century unless they survive by becoming adapted to life in other hosts. For the purposes of our study the cestodes and trematodes are significant as parasites rather than flatworms, since the turbellarians alone are representative of the Platyhelminthes when comparisons are made with other phyla.

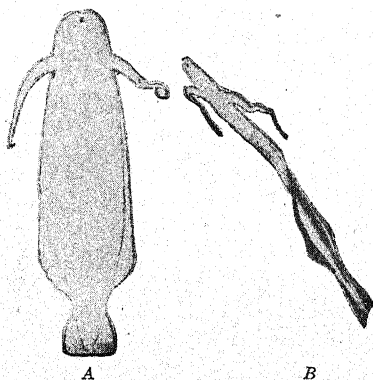


FIG. 256. The pelagic nemertinean, *Nectonemertes mirabilis*. A, ventral view of male; the mouth is visible near the anterior end. B, lateral view of male, showing adaptation for swimming. The tentacles occur only in males and are probably used in sexual union. This worm occurs in the Atlantic Ocean at a depth of five hundred or more fathoms.

(From W. R. Coe and S. C. Ball, 1920, Jour. Morphology, vol. 34.)

The Phylum Nemertinea

Members of the Phylum *Nemertinea* are sometimes called "ribbonworms" because so many of them have greatly elongated, as well as flattened, bodies. Most species are marine, although a few fresh-water and land-dwelling nemertineans are known. They live for the most part burrowing in the bottom or within the growths of animal and plant life upon the bottom; a few are pelagic (Fig. 256 and Fig. 139 M, p. 220). Common American forms are *Cerebratulus lacteus*, which may be several feet long, and *Tetrastemma elegans*, which is less than an inch in length.

The structure of a representative nemertinean is shown by Figure 257. The body is somewhat flattened dorso-ventrally and is ciliated;

the mouth is at the anterior end, the anus at the posterior. A protrusible structure called the proboscis, which lies in a sheath in the dorsal region of the body, is used as a tactile organ and in some species for the capture of prey (Fig. 139 M, p. 220). The digestive tract is a

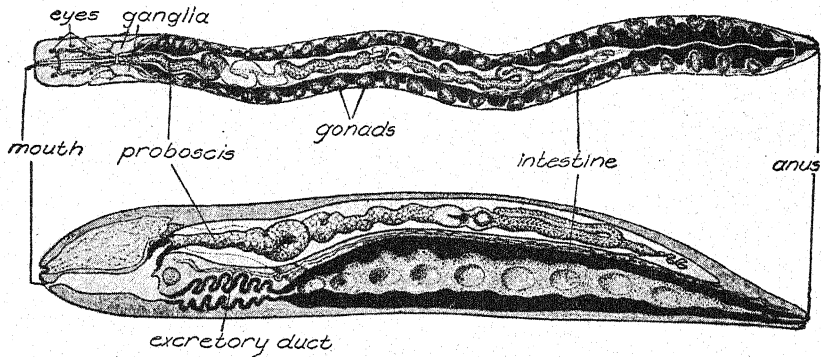


FIG. 257. Internal structure of the nemertinean, *Prostoma græcense*. A, from dorsal view; diagrammatic. B, as if cut in the median, longitudinal plane; diagrammatic.

(From E. Reisinger in P. Schulze, "Biologie der Tiere Deutschlands.")

straight tube with, in most species, many paired lateral pouches. The space between the internal organs is occupied by mesodermal tissue similar to the parenchyma of turbellarians (cf. p. 356). Hence, there is no internal space that can be called a body cavity, or a coelom. The excretory system consists of protonephridia resembling the flame bulbs

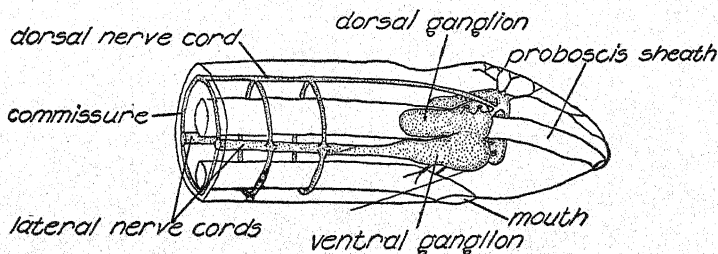


FIG. 258. Anterior portion of the nervous system of a nemertinean, in lateral view; diagrammatic.

(Redrawn from O. Burger in H. G. Bronn, "Klassen und Ordnungen des Tier-Reichs.")

and tubules of Platyhelminthes but more specialized. There is a single dorsal vessel and on each side a lateral blood vessel, which unite at each end of the body; the blood plasma and also the blood cells are colorless. The nervous system consists of two pairs of ganglia, the

"brain," located anteriorly and dorsally, and three longitudinal nerve cords, two lateral and one dorsal, which are connected at different levels by commissures (Fig. 258). There are a number of differentiated sense organs, such as the "eyes" of some species, and special regions of sensory epithelium. The reproductive system consists merely of paired saclike ovaries or testes lying between the lateral pouches of the digestive tract, each opening externally by a separate pore (Figs.

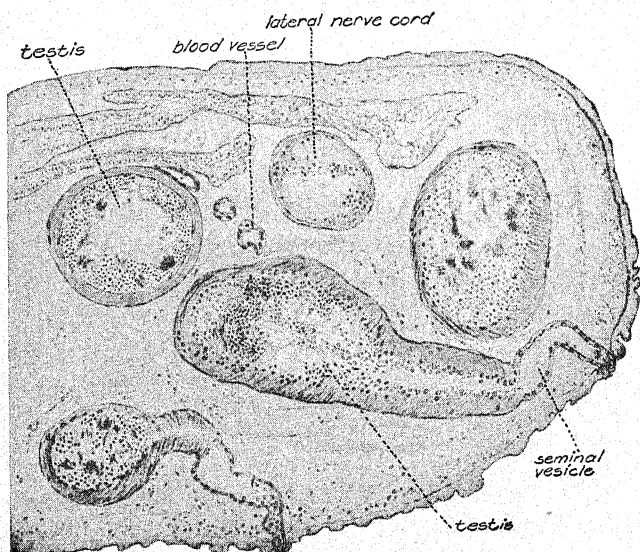


FIG. 259. Reproductive system of the nemertinean, *Nectonemertes mirabilis*; portion of a transverse section of a male, showing four testes.

(From W. R. Coe and S. C. Ball, 1920, *Jour. of Morphology*, vol. 34.)

257 and 259). Some nemertineans are hermaphroditic, but in most species the sexes are separate. According to the species, fertilization occurs within the body of the female or in the open water after the ova and spermatozoa have been discharged. Developmental stages usually include a ciliated, free-swimming larva known as the *pilidium* (Fig. 260), but in a few nemertineans the young develop into miniature adults within the parent (Fig. 261).

The Nemertinea are thus bilateral, triploblastic animals without a body cavity and with protonephridia for excretory organs. To that extent they resemble the Platyhelminthes. On the other hand, they have an anal opening, blood vessels, and a more specialized nervous system. Moreover, the proboscis of the nemertinean is a unique structure, except that an organ somewhat resembling it is found in one

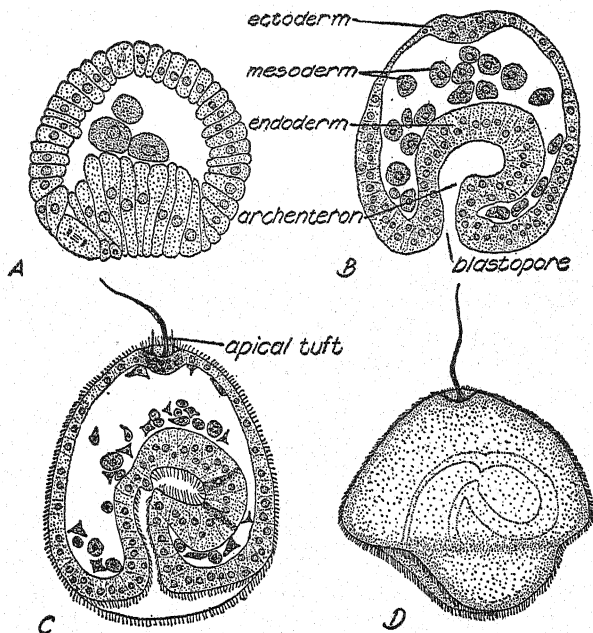


FIG. 260. Development of the nemertean, *Cerebratulus marginatus*. A, median longitudinal section of a late blastula. B, median longitudinal section of a late gastrula. C, median longitudinal section of an embryo at the beginning of the pilidium stage; slightly diagrammatic. D, pilidium, or ciliated free-swimming larva; dotted lines indicate the archenteron.

(Redrawn from W. R. Coe, 1899, Transactions Connecticut Academy, vol. 10.)

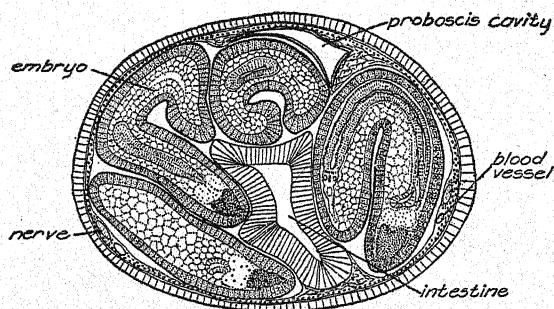


FIG. 261. Transverse section of the terrestrial nemertean, *Geonemertes agricola*, which is hermaphroditic and viviparous. The section, which is through the body of a female, shows four nearly mature embryos; these begin development in the hollow ovaries and eventually fill all the available space between the other organs before they are liberated by rupturing the body wall of the parent.

(From W. R. Coe, 1904, Proceedings Boston Society of Natural History, vol. 31.)

small group of turbellarians. Finally, the development of platyhelminths and nemertineans does not suggest that the two groups are closely related. There seems, therefore, scant justification for classifying these two animal groups within the same phylum. They can be placed together in the Series *Acœlomata* (cf. Fig. 135, p. 215) as animals which are bilateral, triploblastic, and acelomate.

The Flatworm Body-plan

Obviously, the Nemertinea present a more specialized structure than the type found in Platyhelminthes. Within the latter phylum it has been explained that the Turbellaria, rather than Trematoda and Cestoda, are the forms to be used in the construction of any diagrammatic representation of the platyhelminth type (cf. Fig. 233). The Nemertinea may be likewise disregarded because they too are specialized. Hence, the flatworm plan that is important for comparison with the body-plans of other phyla is the turbellarian plan. This plan shows an animal which is triploblastic, or three-layered, with ectoderm, endoderm, and a well-developed mesoderm, in contrast to the diploblastic, or two-layered, organization of a simple coelenterate such as hydra. There is a gut cavity with but one opening, the mouth-anus, and no coelom. The dorso-ventral differentiation, the antero-posterior differentiation with its correlated bilateral symmetry and development of a head, the sensory-neuro-muscular system, and the reproductive system with its complex parts are evidences of greater specialization than anything found in coelenterates. The turbellarian can be compared with a coelenterate, such as a medusa or a shortencd polyp, creeping upon its oral surface, but the more obvious comparisons are with higher animals.

CHAPTER 12

THE ROUNDWORMS AND THEIR RELATIVES: ASCHELMINTHES, ACANTHOCEPHALA, AND ENTOPROCTA

The Phyla *Aschelminthes*, *Acanthocephala*, and *Entoprocta*, to be described in this chapter, have little in common, to judge from superficial appearances. More careful examination shows them to have certain resemblances which lead to their classification as *Pseudocœlomata* (cf. Fig. 135, p. 215), although these resemblances are very general. The name Pseudocœlomata, which means "false cœlom," is applicable because the body cavity of these forms is believed to differ from what may be called the "true cœlom," which is found in more complex animals. The Pseudocœlomata thus differ from the *Acœlomata*, which have no such body cavity, and from the *Eucœlomata*, which have what may be called a "true cœlom" (cf. p. 216).

The Phylum Aschelminthes

Taken as a group, the Phylum *Aschelminthes* must seem to the student a strange assemblage, so diverse do its members appear, even when something is known of their structure. Even the professional zoölogist must be so impressed, although there are good reasons for placing forms as different as rotifers and nematodes within the same phylum. The Aschelminthes include five classes: the Class *Rotatoria*, or rotifers; the Class *Gastrotricha*, a small group of minute animals, representatives of which are often seen in fresh-water cultures; the Class *Echinoderida*, a very small group of minute marine animals; the Class *Nematoda*, which includes the most familiar examples of the roundworms; and the Class *Nematomorpha*, another type of roundworm, of which the "horsehair snake" is an example.

The Class Rotatoria

The Rotatoria are the rotifers, or "wheel animalecules," as they were called by the early microscopists because of the ciliated disks found

in many species. Rotifers abound in fresh water, and a few species are marine. They are microscopic in size, the largest being about $\frac{1}{16}$ inch in length. Although the rotifers are typically free-swimming animals, they may become attached temporarily by a secretion from the posterior end (Fig. 263). A few species live in tubes which are built

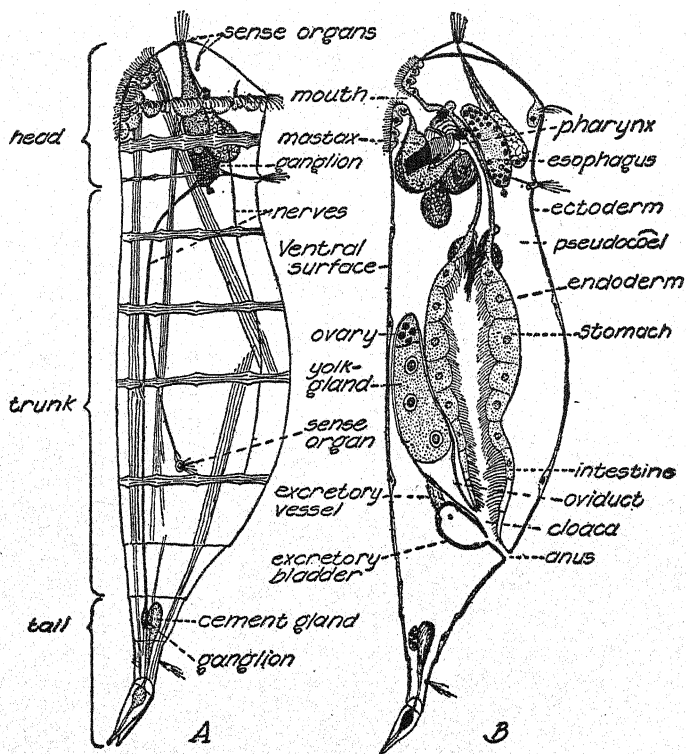


FIG. 262. Structure of a rotifer, from lateral view; diagrammatic. A, sensory-neuro-motor system. B, digestive, reproductive, and excretory systems.

(From A. Remane in H. G. Bronn, "Klassen und Ordnungen des Tier-Reichs.")

by the animal and permanently attached to the substratum (cf. Fig. 141 E, p. 222).

The diversity of structure is so great in the rotifers that a generalized diagram is useful in undertaking a brief description of the structure (Fig. 262). The bilaterally symmetrical animal can be divided into *head*, *trunk*, and *tail* regions; it is covered by a cuticle that is secreted by the ectoderm and is firm enough to maintain its characteristic shape. At the anterior end is the ciliated area, which is responsible for food-getting and in part for the locomotion. In many rotifers

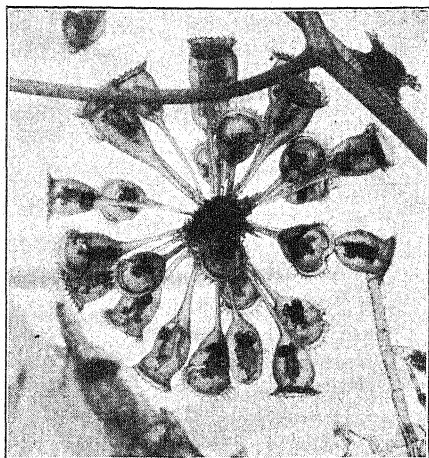


FIG. 263. Cluster of rotifers, *Conochilus hippocrepis*, attached to bit of debris suspended in water.

(Photographed from Rotifer Group in American Museum of Natural History. Courtesy of the Museum.)

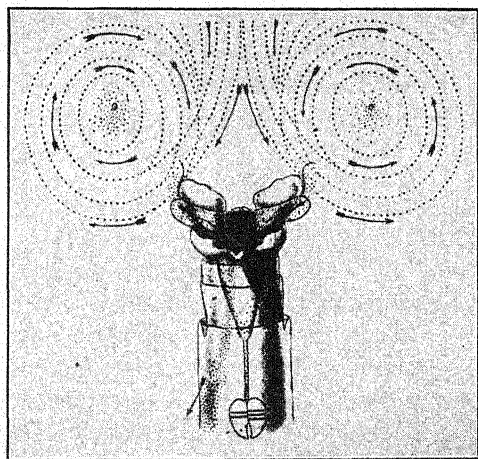


FIG. 264. Anterior end of a rotifer, showing currents of water produced by the cilia.

(From R. Lucks in P. Schulze, "Biologie der Tiere Deutschlands.")

this area is bilobed and suggests two rotating wheels when the cilia are in motion (Fig. 264). At the posterior end is the tail, which has adhesive glands (cement glands) and toe-like processes in many species. The *mouth* is antero-ventral; the *anus*, which is degenerate and non-functional in some rotifers, is postero-dorsal. The *digestive system* includes a pharynx, which contains a "milling" organ called the mastax, an esophagus, a stomach, a short intestine, and a cloaca; cilia may

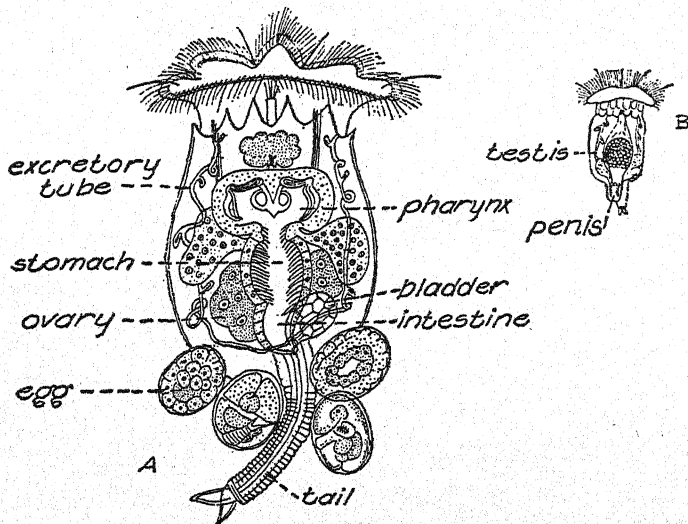


FIG. 265. The rotifer, *Brachionus urceolaris*. A, female with developing eggs attached to posterior end of body. B, male, which is much smaller than female and degenerate.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

occur on the lining of the esophagus, stomach, and intestine (Fig. 262 B). A thin ectodermal layer is found beneath the cuticle, and the middle region of the digestive tract is lined by endoderm. The mesodermal tissue between these layers includes muscle fibers and mesenchyme cells and encloses an ill-defined body cavity (*cf.* p. 216). There is no circulatory system. The *excretory system* consists of flame bulbs and their ducts like those described for flatworms (*cf.* p. 248) and hence of protonephridia. The *nervous system* consists of a large ganglion, which lies dorsally in the head region, and smaller ganglia in other regions of the body. Nerves extend from the ganglia to the sense organs and muscles (Fig. 262 A). The sense organs are distributed over the body but are especially numerous on the anterior end. The sexes are separate. The unpaired *reproductive organs* are

located ventrally. In the female there is a yolk gland and a short oviduct, which opens into the cloaca (Fig. 262 B). The ductus deferens of the male opens on the tail or posterior surface; frequently, there is a penis.

The development of rotifers has been the subject of much investigation. In many species numerous generations of females arise from unfertilized eggs; that is, parthenogenesis occurs, and no males are present. As a result of some change in the environment, eggs that give rise parthenogenetically to males, as well as to females, are produced. These males produce sperm, although in some species the male is so degenerate as to consist only of a testis surrounded by a saclike covering (Fig. 265). The females of such a generation give rise to eggs that must be fertilized before they will develop, and thus a zygote is formed. This zygote, or winter egg, may be surrounded by a protective cyst and remain dormant during unfavorable periods. The complexity that is possible in the life-cycle of a rotifer is illustrated by the life-history that has been recorded for *Hydatina senta* (Fig. 266).

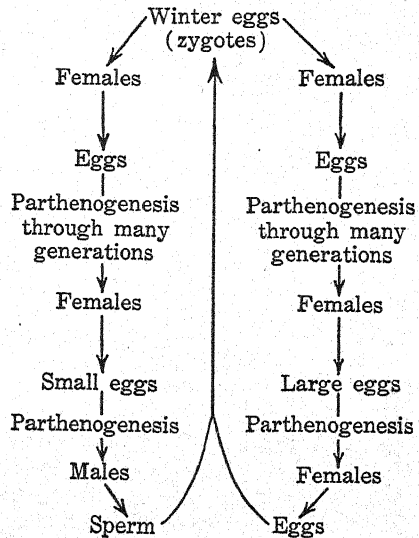


FIG. 266. Life-cycle of the rotifer, *Hydatina senta*.

The Rotatoria are thus important as animals with complex structure and life-cycles and as animals that constitute a significant group among fresh-water organisms. From the standpoint of comparative anatomy they are important in a survey of the Animal Kingdom, because they have a certain resemblance to the trochophore larva found in the Annelida (Fig. 343, p. 363), Mollusca (Fig. 307, p. 425), and several lesser phyla. If this resemblance is the outcome of a common ancestry for all these groups, the Rotatoria represent the survival of an ancestral type. In the adult Rotifera this type is much specialized but is still comparable with a trochophore. In the phyla having a trochophore larva the adult is a very different kind of animal but is derived in its individual development from a trochophore larva, which, if the "trochophore theory" is correct, presents the tell-

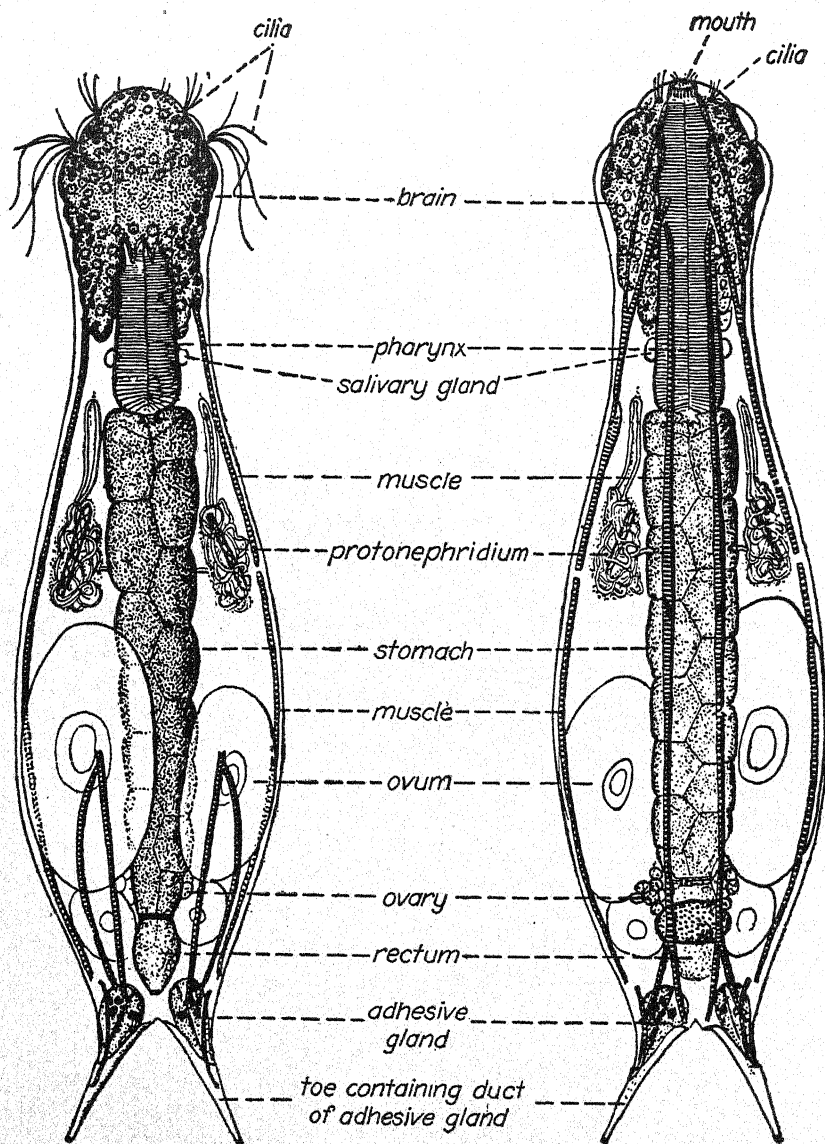


FIG. 267. The gastrotrich, *Chætonotus*; diagrammatic. Left, dorsal view. Right, ventral view.

(After Zelinka, from A. Remane in W. Kükenthal, "Handbuch der Zoölogie.")

tale evidence of ancestry. The hypothetical relationship between an ancestral trochophore and its possible descendants is shown in Figure 150, p. 233.

The Class Gastrotricha

The minute animals comprising the Class *Gastrotricha* are sometimes classified with the rotifers, but they are better placed in a class by themselves. They have, like the rotifers, resemblances to the roundworms which justify their inclusion within the Phylum Aschelminthes. Representative of the gastrotrichs common in fresh water are species of the Genus *Chaetonotus* (Fig. 267).

The chaetonotus is covered with a firm cuticle having many projecting spines. Cilia located upon the ventral surface bring about the locomotion. At the anterior end there are longer cilia which have tactile as well as vibratile functions. The mouth is at the anterior, the anus at the posterior, end; and the digestive tract consists of a pharynx and an intestine. There are no organs of circulation. As in the flatworms and rotifers, there are flame bulbs and ducts, called protonephridia, which open externally and which are regarded as the excretory organs. The body cavity is ill-defined, consisting merely of the spaces between the internal organs, and is, therefore, a pseudocœl (cf. p. 216). There is a relatively large mass of nervous tissue, located dorsally at the anterior end, which is called the "brain" and from which a nerve cord extends for some distance posteriorly on each side. Sense organs are present as sensory hairs located on various parts of the body. Pigment spots at the anterior end in some species have been called "eye-spots," but it is not clear that these spots have a light-perceiving function. The musculature consists of specialized bands somewhat resembling those of rotifers. The sexes are separate in some species, but hermaphroditism is known in others. Parthenogenesis seems to be common, and there are species in which no males have been found.

The Class Echinoderida

The Class *Echinoderida* is a small group of minute marine animals, evidently related to the Rotatoria and Gastrotricha. The outer surface is not ciliated but is provided with numerous spines, which are especially developed at the two ends of the body (Fig. 268). The body is covered with a firm cuticle and is divided into eleven or twelve rings, giving an appearance of metamerism but not regarded as evidence of this condition. A transverse section shows the dorsal surface to be strongly convex and the ventral surface flat or slightly con-

cave. The mouth lies at the end of a protrusible anterior region which is very mobile and furnished with conspicuous spines, and the anus is located at the posterior end between paired spines. The digestive tract consists of a pharynx and an intestine. There are no organs of

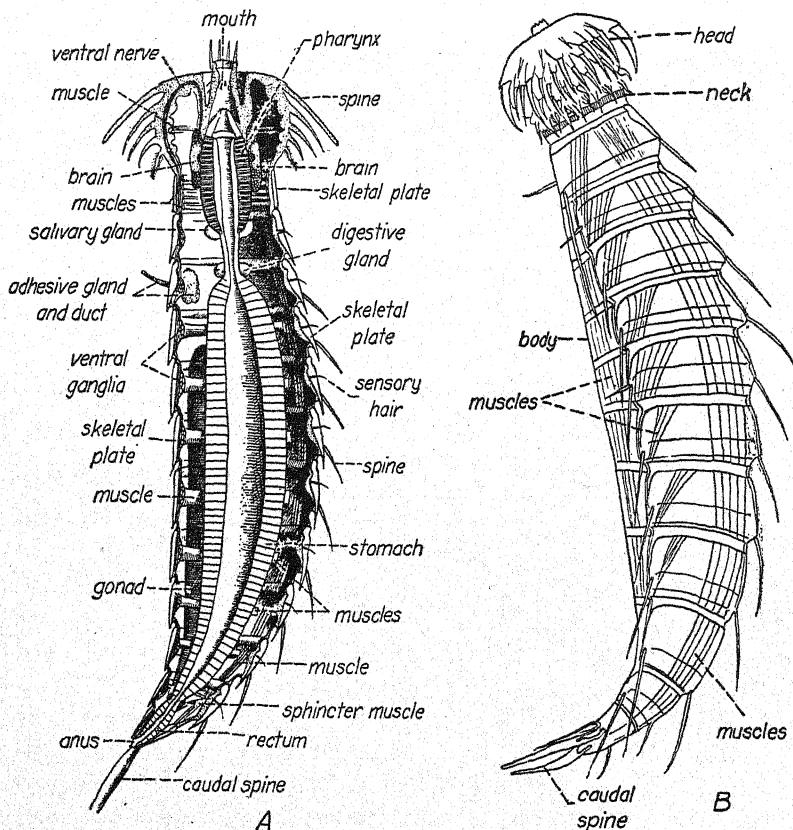


FIG. 268. Echinoderida. A, diagrammatic longitudinal section. B, external features of *Campyloderes vanthöffeni*, lateral view.

(From A. Remane in W. Kükenthal, "Handbuch der Zoölogie.")

circulation. As in rotifers and gastrotrichs, there is a system of flame bulbs and ducts, called protonephridia, which are presumed to have an excretory function. The body cavity is a pseudocœl, since it consist merely of the spaces between internal organs. A ring of nervous tissue, the so-called "brain," surrounds the pharynx and is connected with a ventral nerve cord. Paired eye-spots are found dorsal to the brain, and there are sensory spines upon the surface of the body. The musculature is highly developed as muscle bands related to the move-

ments of the body rings, the spines, and the protrusible anterior end. The sexes are separate, and the reproductive organs are paired glands with ducts opening right and left of the anus. Manifestly, the echinoderes have certain very characteristic features. One can understand why students of the group place them in a class by themselves.

The Class Nematoda

Free-living Nematoda. The Class *Nematoda* is known principally through its parasitic species, which have long been familiar. Only recently has it been appreciated that there are, in addition, many species of free-living nematodes which occur in salt and fresh water and in moist soil (Figs. 269 and 270). They exhibit great diversity of

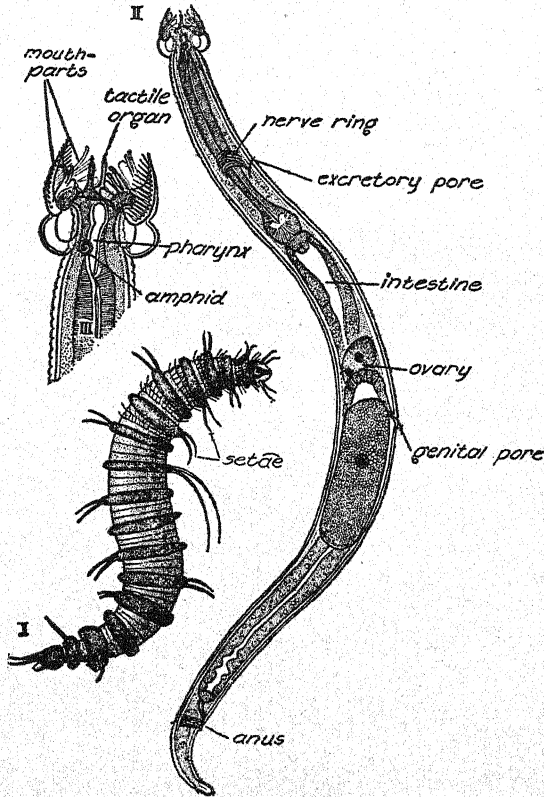


FIG. 269. Free-living nematodes. I, the banded nematode, *Desmoscolex*. II, lateral view of the female of a soil nematode, *Wilsonema* ($\times 600$). III, lateral view of the head of *Wilsonema* ($\times 1230$).

(From N. A. Cobb, 1914, Yearbook U. S. Dept. Agriculture.)

structure in contrast with the parasitic species, which show the simplifications characteristic of parasites (Fig. 271 A). For example, the head and mouthparts of a free-living nematode may be highly specialized in correlation with the mode of life, whereas this region in the parasitic species is much simpler, although it may be well suited to the needs of the parasite. In the free-living forms organs of chemical sense, sometimes called amphids, are practically universal, and tactile organs and eyes occur in some species. The skeletonlike cuticle, which is universally present, is molted periodically like the skeleton of an

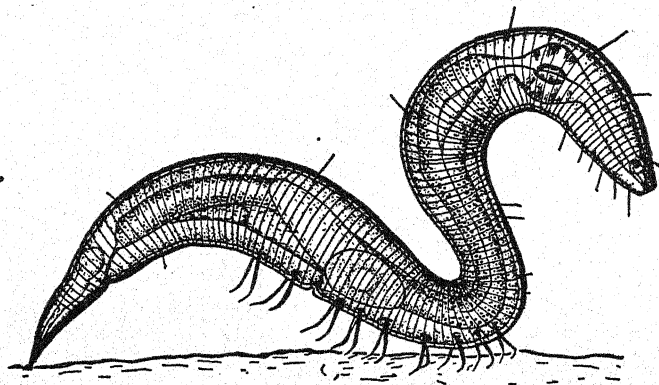


FIG. 270. The free-living nematode, *Rhabdogaster*, in locomotion.

(From M. Rauber in W. Kükenthal, "Handbuch der Zoologie.")

arthropod (cf. p. 501). Most species are capable of active locomotion by body movements, and locomotor appendages are found in many instances. The occurrence of striated muscle is to be correlated with the active movements. The nervous system, which consists of a circumpharyngeal ring, from which nerve cords extend posteriorly, is not elaborate, but the sensory-neuro-muscular system must be effective in view of the activities to be observed. The internal structure is much more complex than that of parasitic nematodes. Since the free-living representatives of the phylum are not commonly studied, we shall examine a few of the parasitic species as further examples of parasitism. Some of these have complex life-cycles, with alternation of hosts.

Parasitic Nematoda. *Ascaris lumbricoides*. The adult worm, which lives in the human digestive tract, is hardly distinguishable from the *Ascaris* found in swine, which is probably another variety of the same species (Fig. 271). The female is about 8 to 16 inches and the male some 6 to 8 inches in length. At the anterior end is the *mouth*,

bounded by two ventro-lateral lips and one dorsal lip. The smooth cylindrical body is marked with four *longitudinal lines*, dorsal, ventral, and lateral. Near the posterior end on the ventral side is the *anus*. In the female the reproductive opening, or *genital pore*, lies on the ventral midline about one-third the length of the body from the anterior end, whereas in the male this opening is just within the

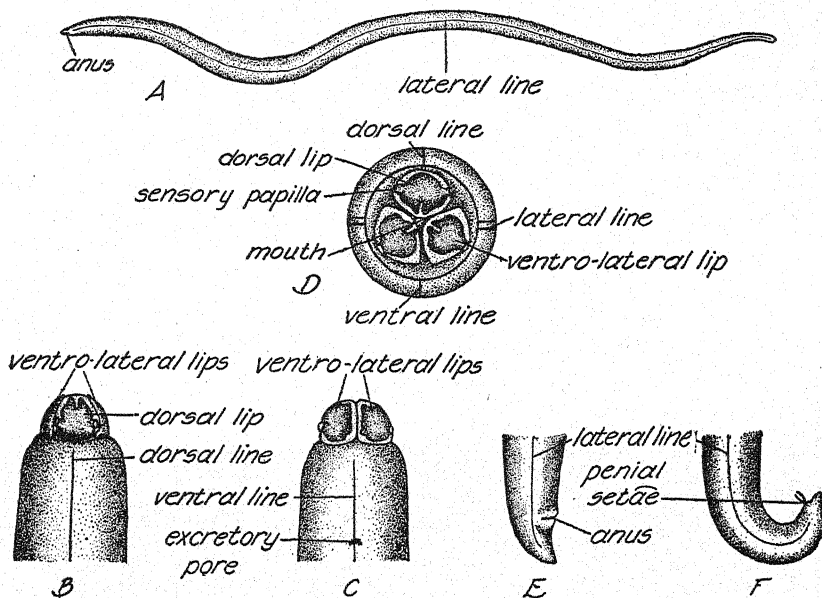


FIG. 271. External features of the parasitic nematode, *Ascaris lumbricoides*. A, female, viewed laterally. B, anterior end, dorsal. C, anterior end, ventral. D, anterior end, viewed anteriorly. E, posterior end of female, lateral. F, posterior end of male, lateral.

(Redrawn, with modifications, from R. Leuckart, "Die menschlichen Parasiten," 1876.)

posterior end of the digestive tract (Fig. 272 C). The single *excretory pore* is located on the ventral midline a short distance posterior to the mouth (Fig. 271 C).

The internal structure, like the external, does not show the differentiation seen in free-living nematodes, although the general plan of the nematode body may be illustrated by the structure found in *Ascaris* (Fig. 272 A and B). The non-cellular cuticle, the epidermis, the muscle and other mesodermal tissues of the body wall, and the digestive tract with its lining of endodermal epithelium should be compared with the corresponding structures of other animals (*cf.* Figs. 211, 233, and 342, pp. 211, 346, and 461). The spacious body cavity is

a *pseudocœl*, or false cœlom, because it lacks the features characteristic of the cœlom in animals such as the annelids and the vertebrates (*cf.* p. 216). The *digestive tract* is differentiated into a pharynx, which has a muscular wall, an intestine composed of endoderm bounded by two layers of cuticle (Fig. 272 B), and a rectum, in which the endoderm is surrounded by a few muscle cells. In *feeding*, the intestinal content of the host is drawn into the pharynx, which is muscular, and passed to the intestine of the ascaris. Here, the food is presumably absorbed into the body cavity to become part of the fluid of this cavity. No digestive glands are necessary because the food has been predigested by the host. The only *circulatory mechanism* is the transfer of material in the body-cavity fluid, which bathes, and so can nourish, all parts of the worm.

The *respiration* differs from that of animals having access to the free oxygen necessary for most species. There is little such oxygen in the intestinal cavity of the host. The respiration of an ascaris follows a chemical pattern known as *anærobic respiration*, in contrast to the *ærobic respiration* which has been described (*cf.* p. 48). The nature of the chemical changes involved in anærobic respiration is not clear and may not be the same in all cases. Perhaps this process occurs in more of the cold-blooded vertebrates and of the invertebrates than has been supposed. Animals found in mud and slime live under oxygen conditions not unlike those within the intestinal cavities that harbor such parasites as the ascaris.

The *excretory system* is composed of two tubules, one lying in each lateral line and the two uniting anteriorly to open by the excretory pore (Fig. 271 C). These tubules do not have flame bulbs; they are not ciliated like protonephridia (*cf.* p. 348); and they do not have openings into the body cavity, as do the nephridia of invertebrates (*cf.* p. 567). Each tubule consists of a single elongated cell with one nucleus and an intracellular cavity. It is supposed that the mechanism functions by extracting soluble excretory matter from the body-cavity fluid and passing it to the outside. The *nervous system* consists of a circumpharyngeal ring and longitudinal nerve cords (Fig. 272 A and B).

The *cellular organization* of the ascaris is quite unlike that found either in the flatworm (Fig. 246, p. 355) or in segmented worms, such as the earthworm (*cf.* Fig. 342, p. 461). The body wall consists of an external cuticle, a syncytial layer called the ectoderm, and a layer of very specialized epithelio-muscular cells, which constitute the musculature of the body wall and line the body cavity. The gut wall consists of a single layer of endoderm cells covered externally and

internally with a thin cuticle. The *reproductive organs* are simple tubes, blind at their inner ends and lying free in the body cavity except for their attachment where they open externally. The female system

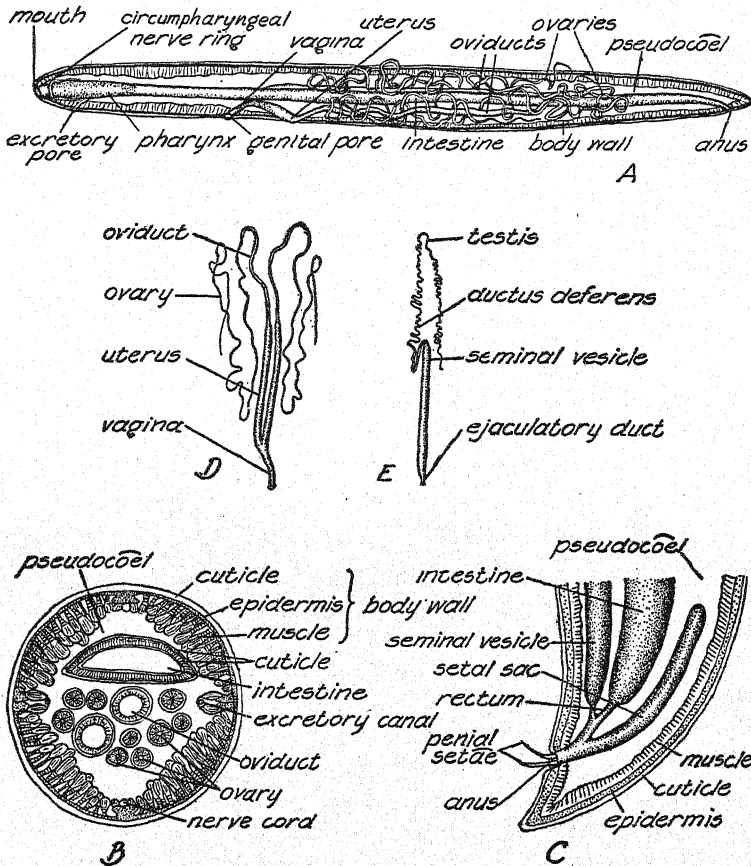


FIG. 272. Internal structure of *Ascaris lumbricoides*. A, dissection of a female, from lateral view; diagrammatic. B, cross section of body in the mid-region. C, longitudinal section of posterior end of the male. D, female reproductive system. E, male reproductive system.

(Redrawn, with modifications, from R. Leuckart, *op. cit.*)

is composed of paired ovaries and the oviducts, which expand to form the uteri and unite in a short terminal portion, the vagina (Fig. 272 D). The male system is a single tube differentiated into a testis, a ductus deferens (vas deferens), and a terminal portion which serves for storage of the mature spermatozoa and may be called the seminal vesicle

(Fig. 272 C and E). Near the external opening of the male system is a pair of spinelike structures, the penial setæ, that presumably is used during copulation.

The spermatozoa (Fig. 273 B), which are introduced into the vagina of the female at the time of sexual union, fertilize the ova within the oviducts. The zygote formed by the union of ovum and spermatozoön becomes surrounded by a resistant shell, like the cyst of a protozoan or the eggshell of a cestode (Fig. 273 A). The "eggs" thus formed are discharged from the parent worm and pass from the digestive tract of the

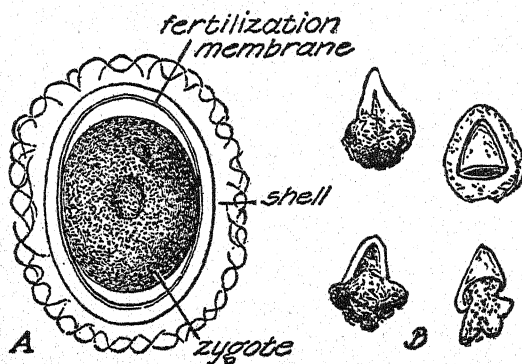


FIG. 273. Fertilized egg (A) and amœboid sperm (B) of *Ascaris lumbricoides*.

(From R. Leuckart, *op. cit.*)

host with the feces. If the environmental conditions are unsuitable, the development may be delayed for months and perhaps for several years. If the conditions are suitable, development begins immediately after the egg leaves the host and proceeds until a small worm is formed (*cf.* Fig. 275), although hatching does not occur unless the egg is swallowed with the food or drink of a new host. When the egg thus reaches the small intestine of man, the young worms hatch, penetrate the mucous membrane, and return to the digestive tract after a journey that may include the blood stream, liver, heart, lungs, and trachea. Some growth occurs during this migration, but the worm is still small when it reënters the digestive tract, and the adult size is not attained until it has been in the intestine for some time. Infection of man by *Ascaris lumbricoides* is not uncommon and is sometimes serious, being complicated by the fact that the adult worms sometimes wander from their usual location in the intestine to the stomach, from which they may be vomited, or they may even work their way up to the esophagus of the host and emerge from the mouth or nose.

Necator americanus. The adult stage of this parasite, which is the hookworm of the southeastern United States, is found attached firmly to the wall of the human intestine, often in large numbers. Males are

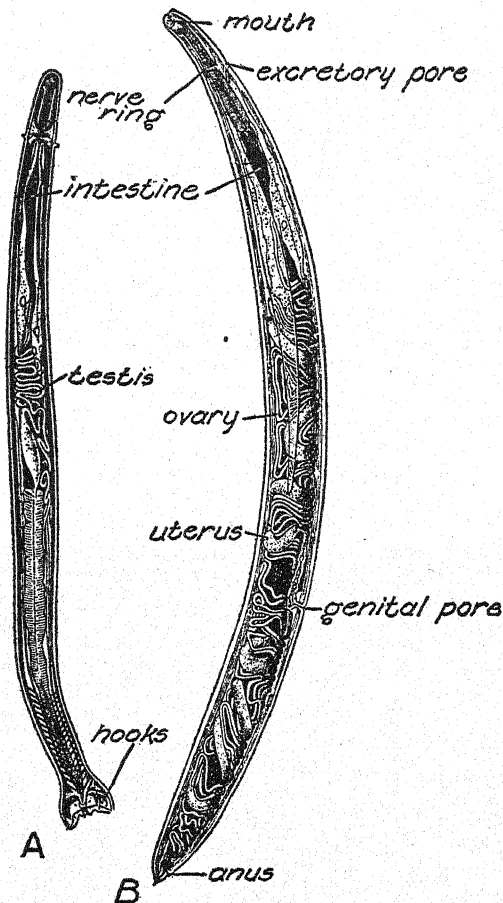


FIG. 274. The Old-World hookworm, *Ancylostoma duodenale*, showing internal structure. A, male. B, female.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

about $\frac{3}{8}$ inch in length, and the females slightly larger. The name hookworm, derived from the hooks at the posterior end of the male, by which the female is held during sexual union, is also appropriate in relation to the hooklike teeth that occur within the mouth cavity in both sexes. Aside from the hooks, there is nothing in the external structure that is distinctive, since the smooth cylindrical body re-

sembles that of many other parasitic nematodes. The internal structure is essentially like that of *Ascaris*. The Old-World hookworm, *Ancylostoma duodenale* (Fig. 274), also occurs in America, although it is not so common as *Necator americanus*. The two genera differ in only minor characters, such as the shape of the body, the mouthparts, the position of the genital pore in the female, and the structure of the copulatory organs in the male.

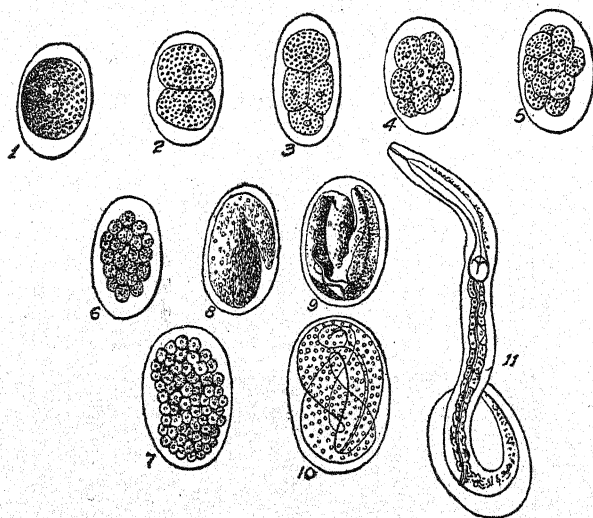


FIG. 275. Development of the hookworm, *Ancylostoma duodenale*. 1-7, stages in segmentation of the egg. 8-10, early embryos. 11, young worm, hatching.

(From C. W. Stiles, 1902, 18th Annual Report, Bureau Animal Industry, U. S. Dept. Agriculture.)

In *Necator*, spermatozoa are transferred to the female during sexual union, and fertilization occurs within the oviducts. The zygote is surrounded by a shell and then discharged into the host's intestine, from which it passes with the feces (*cf.* Fig. 275). Small worms hatch from these eggs and are found migrating through the soil during the free-living stages that follow. As a result, the worms may be distributed over an area several feet in diameter by their own activities and may also be transported accidentally. New hosts are usually infected by penetration of the skin of the feet, although the parasites readily penetrate the skin on other parts of the body. After such an entrance they migrate by way of the lymph and blood vessels to the lungs and thence to the trachea and esophagus, from which they pass into the intestine, where they reach the adult stage. The hookworm is a dangerous parasite, because it occurs in great numbers and each worm

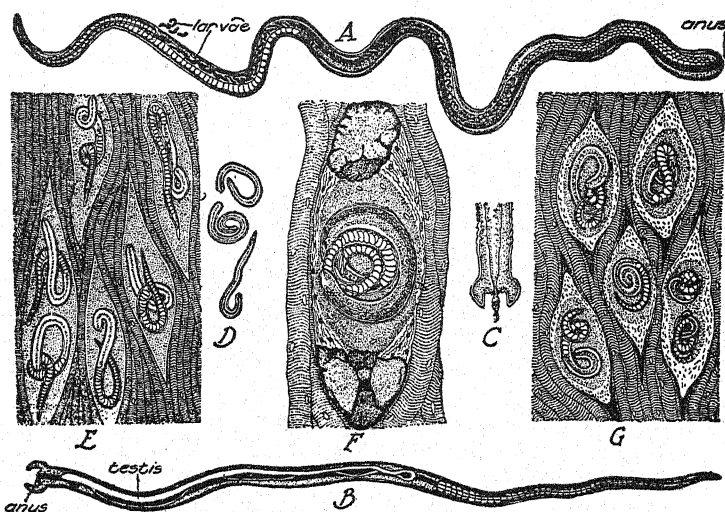


FIG. 276. Structure and life-cycle of the trichina worm, *Trichinella spiralis*. A, female. B, male. C, posterior end of male, showing the single hook. D, new-born larvæ. E, F, and G, larvæ embedded in muscle; in F and G, cysts have been formed around the larvæ.

(From G. Wülker in P. Schulze, "Biologie der Tiere Deutschlands.")

feeds on the mucosa at different places in the intestinal wall, with the result that much blood may be lost by the host. Its effect is not likely to be fatal, except as the patient becomes weakened and succumbs to other diseases. The immediate effects appear in the loss of efficiency and lowered resistance to disease. The infection of large numbers of the rural population in certain sections of the southeastern United States still presents a serious hygienic and economic problem, although the adult worms can be expelled from the digestive tract by proper treatment, and the sanitary disposal of feces and the wearing of shoes are effective in preventing infection.

Trichinella spiralis. Unlike most species of parasites, this nematode can live in a number of hosts, including man. The adult worms are minute (females about $\frac{1}{8}$ inch, males less than $\frac{1}{16}$ inch in length) and are found in the intestine among the folds of the mucous membrane (Fig. 276 A and B). As the earliest

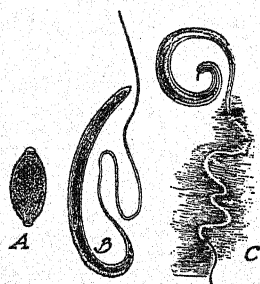


FIG. 277. The whipworm, *Trichuris*. A, egg. B, female. C, male, with whiplike anterior end embedded in mucous membrane of the host.

(From R. Leuckart, "Die menschlichen Parasiten," 1876.)

stages of development and the hatching occur within the oviducts of the parent, small worms, instead of eggs, are discharged from the female. These young individuals do not pass out with the feces but bore through the mucous membrane and into the blood vessels of the host. They are then carried to other parts of the body, where they pass through the walls of the capillaries and enter the tissues, particularly the muscle cells. In this location the parasites become surrounded by cysts and develop to the late juvenile stages (Fig. 276 E-G). They do not become adults unless the tissue in which they are contained is eaten by another animal which can serve as a host. When they thus reach the intestine of a suitable host, the cycle is repeated. If the juvenile stages remain in the muscle, they eventually die without doing serious injury to the host unless they are present in large numbers. However, the life-cycle is such that heavy infections of both intestine and muscle are likely to occur. The result of such an infection is usually fatal. Man most commonly becomes a victim by eating infected pork that has been insufficiently cooked. Swine become infected by eating the flesh of other animals, since *Trichinella* parasitizes many species of mammals.

Other Parasitic Nematodes. Among other nematodes that occur as parasites in man are the whipworm *Trichuris* (Fig. 277) and the pinworm *Enterobius vermicularis* (Fig. 278), found in the human intestine, and the filarial worms, *Wuchereria bancrofti* (*Filaria bancrofti*) and *Dracunculus medinensis* (*Filaria medinensis*). The filarial worms are of interest because they are the only parasitic nematodes that require an intermediate host in order to complete the life-cycle (cf. Fig. 186, p. 280). The adult female of *W. bancrofti* varies from 2½ to 4 inches in length and is very slender; the male is about half as large as the female. The adult individuals live in the lymph glands of man, and reproduction cannot occur unless specimens of opposite sex happen to reach the same gland. If fertilization occurs, development takes place in the uterus of the female; and when the young, which are known as micro-

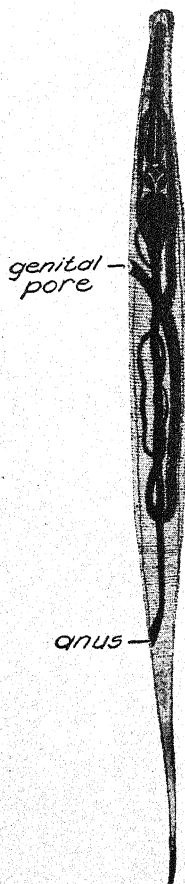


FIG. 278. The pinworm, *Enterobius vermicularis*. Female, with digestive and reproductive systems shown in black.

(From M. Rautner in W. Kükenthal, "Handbuch der Zoologie.")

filariæ, are shed, they make their way into the blood stream (Fig. 279 A and B). No further development is possible unless the microfilaria are sucked into the stomach of a mosquito. Each microfilaria can then migrate from the stomach of the mosquito to its wing muscles, where a metamorphosis occurs (Fig. 279 C). After about 10 days the larva moves into the proboscis of the mosquito and is ready to crawl onto the

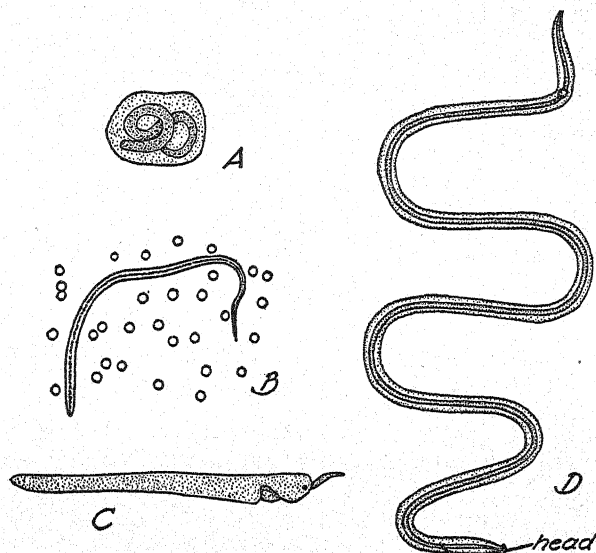


FIG. 279. Life-cycle of *Wuchereria bancrofti*. A, late embryo. B, larva (microfilaria) in blood of man; the circles represent red blood cells. C, larva from thoracic muscles of mosquito. D, larva at time of escape from proboscis of mosquito.

(A, redrawn from M. Rauter in W. Kükenthal, "Handbuch der Zoölogie"; B, from W. Stempel, "Zoölogie im Grundriss," 1926; C and D, redrawn after E. Francis, from R. Hegner, F. M. Root, and D. L. Augustine, "Animal parasitology," 1929, The Century Co., printed by permission.)

skin of a man while the mosquito is feeding (Fig. 279 D). After puncturing the skin, the larva enters the lymphatic system and lodges in a lymph gland, where the adult stage is reached. The microfilaria are apparently not toxic to man, but the adults, if present in large enough numbers, may clog the lymph passages and so produce a lymph oedema, or swelling. Elephantiasis is one serious condition that may result from heavy infestation with *W. bancrofti* (Fig. 280 B).

The *Dracunculus medinensis* is known as the guinea-worm and was probably the "fiery serpent" mentioned by Moses. The female is about 3 feet in length and $\frac{1}{32}$ inch in width. Few males have

been found; they are much smaller than the females. The female worm containing numerous larvæ comes to lie in the subcutaneous connective tissue (Fig. 280 A). A small ulcer appears on the skin near the head of the worm. If water is placed on such a region of the skin, the female discharges the larvæ through the genital opening, which is located at the anterior end. These larvæ can develop farther only

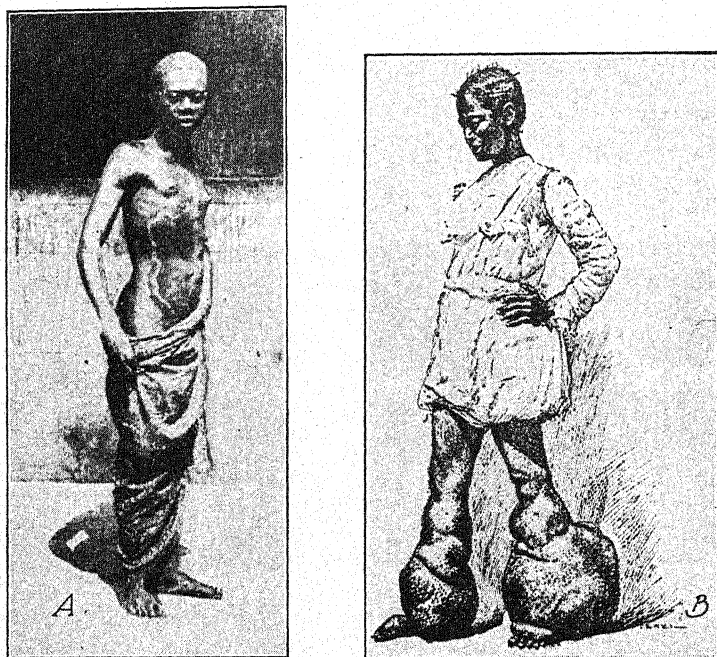


FIG. 280. A, *Dracunculus medinensis* beneath the skin of chest and abdomen in man. B, elephantiasis of the lower limbs, due to *Wuchereria bancrofti*.

(A, after J. W. S. Macfie; B, after L. W. Sambon, from R. Hegner, F. M. Root, and D. L. Augustine, *op. cit.*, reprinted by permission.)

if they can find and enter a small crustacean belong to the Genus *Cyclops*. Within this host metamorphosis occurs, and after 4 to 6 weeks the larvæ can infect a man who swallows the cyclops in his drinking water. It is apparently about a year before the worm becomes adult and reaches the skin. No serious effects result from this parasite unless unsuccessful efforts are made to extract it. If the worm is broken and the larvæ are freed in the tissues, severe poisoning follows. Although the filarial worms are typically tropical parasites, they were widely distributed during the days of slave trading. Control of mosquitoes and sanitary sources of drinking water are effective in preventing infection of man by these parasites.

The Class Nematomorpha

The Nematomorpha, or hairworms, are roundworms with greatly elongated bodies varying in length from an inch to 5 feet in different species. A description of the Genus *Gordius* will serve as a character-

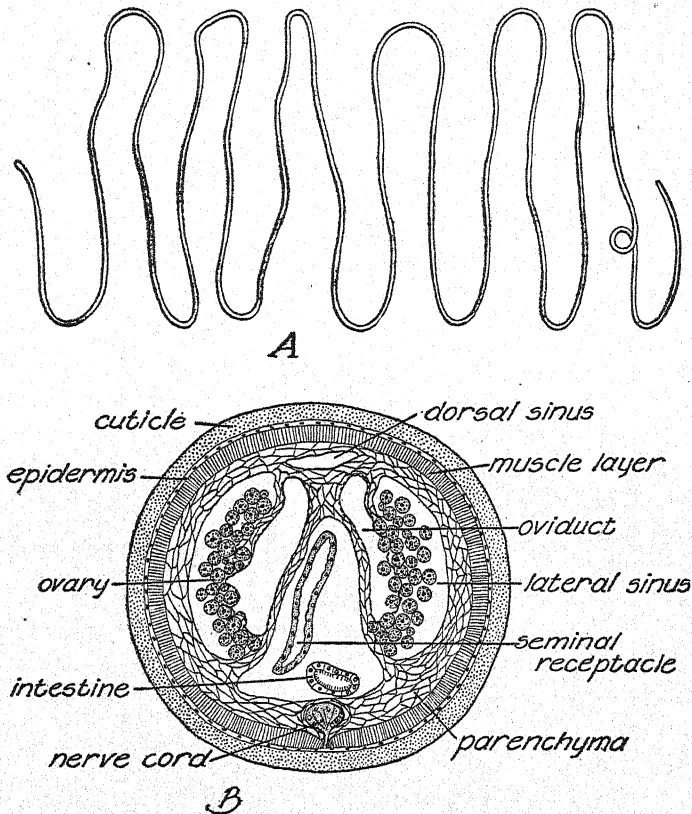


FIG. 281. Structure of the "horsehair snake," *Gordius*. A, external view of adult *G. aquaticus*. B, cross section of body of *G. tolosanus*.

(A, from M. Rauter in W. Kükenthal, "Handbuch der Zoölogie"; B, redrawn, with modifications, from M. Rauter, 1905, *Jenaische Zeitschrift für Naturwissenschaft*, vol. 40.)

ization of the group (Fig. 281 A). The adult of this species, which is called the "horsehair snake," occurs free-living in fresh water; the larval stages occur as parasites in the bodies of aquatic insects. In the adult worm the *intestine* is a straight tube opening by way of the *anus* at the posterior end; there is no mouth. Certain Nematomorpha

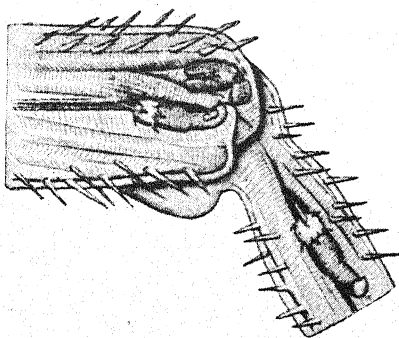


FIG. 282. Larvæ of the hairworm, *Parachordodes tolosanus*, between the leg muscles of a may-fly larva (cf. Fig. 283 and Fig. 373, p. 504).

(From M. Rautner in W. Kükenthal, "Handbuch der Zoölogie.")

have a *mouth*; in still others the tract is practically absent. The body is covered with a cuticle beneath which is the epidermis and a layer of muscles except at the ends of the body (Fig. 281 B). The body cavity (cf. p. 216) consists of four longitudinal spaces or sinuses within the parenchyma; in the adult female the two lateral cavities are lined with a peritoneum. Circulatory and excretory organs are absent. The *nervous system* consists of an anterior nerve ring and a mid-ventral nerve cord. Sense organs are represented by what are probably primitive eyes and also by isolated sensory cells. The sexes are separate, and the *reproductive organs* open into the posterior end of the digestive tract. Fertilization occurs in the body of the female, and the eggs are laid from the anus in long strings. Development thus begins in

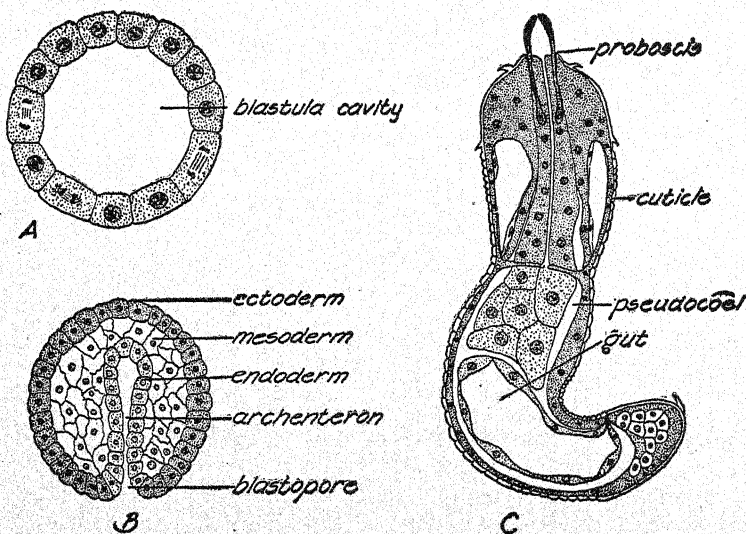


FIG. 283. Development of *Gordius aquaticus*. A, blastula. B, late gastrula. C, longitudinal semidiagrammatic section of the free-living larva which will enter an insect larva (cf. Fig. 282).

(Redrawn from A. Mühlendorf, 1914, Zeitschrift für wissenschaftliche Zoölogie, vol. 3.)

the water (Fig. 283). When the young worms hatch, they swim about until they die or succeed in boring into the larva of some aquatic insect (Fig. 282). After this transfer development continues in the body cavity of the new host; and eventually the juveniles, as these early adult stages are called, escape from the insect. The sudden appearance of individuals which have thus emerged from their hosts has given rise to the popular belief that the hairworms come from horse-hairs placed in water.

The Aschelminth Body-plan

Even after the foregoing survey it may seem strange that animals so different as those making up the five classes of the Aschelminthes should be placed in the same phylum. The Rotatoria, Gastrotricha, and Echinoderida have clear resemblances. But how can these three classes be compared with the Nematoda and Nematomorpha? It will be recalled that a similar, although less serious, difficulty is presented by the Platyhelminthes when comparisons are attempted between the free-living Turbellaria and the parasitic Cestoda. If there were no Trematoda with their evident resemblances to the Turbellaria, it would perhaps seem difficult to classify the turbellarians and the cestodes in a single phylum. In comparing the several classes of the Phylum Aschelminthes, it is helpful to consider the resemblances between the free-living nematodes and the rotifers, gastrotrichs, and echinoderes. When this is done, the nematodes and the members of these other classes seem to have more in common, although the free-living nematodes present their own characteristic features. Such a form as *Rhabdogaster* (Fig. 270) can be thought of as an animal related to the rotifers, gastrotrichs, and echinoderes, although specialized in its own way. And this is how the zoölogist thinks of the free-living nematodes when he follows the classification used in this textbook. The parasitic Nematoda and the Nematomorpha are then regarded as animals still further specialized in ways related to their parasitic mode of life.

The Phylum Acanthocephala

Adults of the Phylum *Acanthocephala* are roundworms that vary from a small fraction of an inch to 18 inches in length and occur as parasites in the intestines of vertebrates; their larvæ are parasitic in the bodies of invertebrates, especially crustaceans. At the anterior end of the adult worm is a proboscis that is armed with hooks and serves for attachment to the host (Fig. 284). There is no trace of a digestive

tract at any stage of development. The only external opening is that of the reproductive system at the posterior end. The sexes are separate. Development is unusual in that neither blastula nor gastrula

cavities are formed. An outer layer of cells, the ectoderm, and a central mass of cells, the so-called endoderm, result from cleavage. The central mass of cells splits to form an outer layer from which the muscles arise and an inner layer from which the other internal parts develop, leaving a cavity that can be called a body cavity but not a coelom (cf. p. 216). Additional species of Acanthocephala are being discovered, and these worms may eventually become known as a much larger group. The position of the Acanthocephala in classification is problematic, but they seem to be forms without a true coelom and hence to be classified with other such groups as Pseudocoelomata.

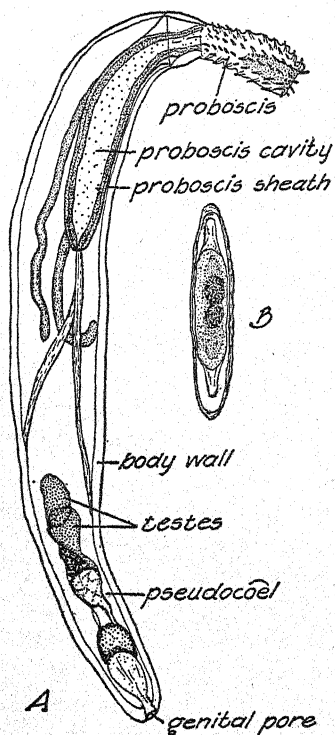


FIG. 284. The spiny-headed worm, *Echinorhynchus thecatus*. A, optical section of an immature male, showing the internal structure. B, an embryo from the body cavity of a mature female.

(Slightly modified from H. J. van Cleave, 1919, Bulletin Illinois Natural History Survey, vol. 13.)

The Phylum Entoprocta

The Entoprocta are small, attached animals that, in the great majority of the species, form colonies by budding. Less than a dozen genera are known, all of them marine except the American Genus *Urnatella*, which lives in fresh water. They have been classified as Bryozoa (cf. p. 399), but this is open to criticism. It seems better to classify them as a small phylum and to group them as Pseudocoelomata along with the Aschelminthes and the Acanthocephala (cf. Fig. 135, p. 215). Familiar genera are *Loxosoma* and

Pedicellina (Fig. 285). Although *Loxosoma* reproduces by budding, the buds soon become detached, and thus the members of this genus seem to be solitary. In *Pedicellina* the buds remain attached and colonies are formed, as in most Entoprocta.

In the case of *Loxosoma* (cf. Fig. 285), the adult consists of a

bilaterally symmetrical body having a ring of tentacles encircling the mouth and also the anus, and of a stalk by which the animal is attached. The arrangement of the distal parts differs from that in the Bryozoa, where the anus lies outside the ring of tentacles (*cf.* Fig. 287,

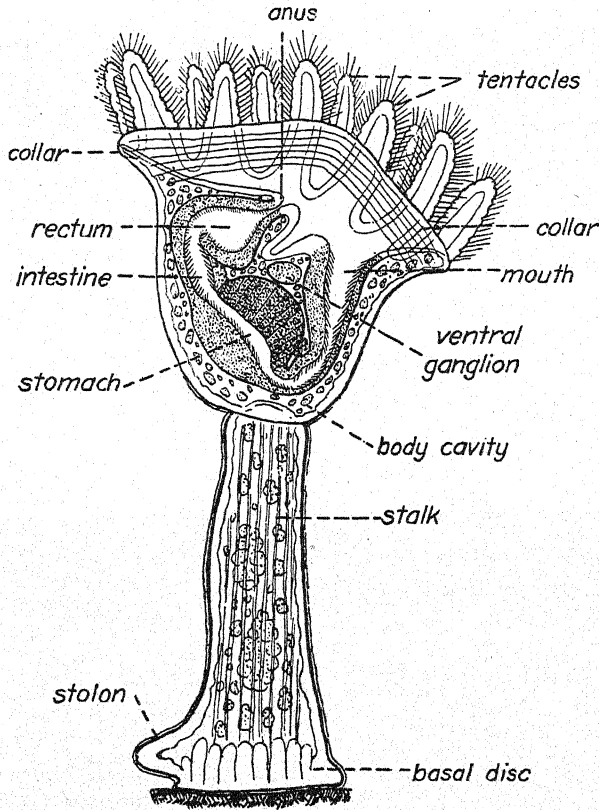


FIG. 285. Young individual of *Pedicellina cernua*, a representative of the Entoprocta. The stolon grows out and forms buds, thus producing a colony of many individuals, which constitutes the adult stage.

(From C. J. Cori in W. Kükenthal, "Handbuch der Zoologie.")

p. 400). The short digestive tract is thus U-shaped, and the region between mouth and anus, to judge from the development, is to be called the ventral region. There are no organs of circulation. The protonephridia consist of a pair of flame bulbs with ducts which unite before opening externally on the midline between mouth and anus. The body wall and gut walls consist of epithelial cells, without muscle cells or peritoneum. The body cavity consists merely of the space between

gut and body walls and within the stalk and tentacles and is, therefore, a pseudocœl; it contains mesenchymatous and amœboid cells. There is a bilobed ganglion, located in the ventral region between mouth and anus, from which nerves extend to the tentacles and other parts including a pair of sense organs. The rudiment of a dorsal ganglion is present during the larval stage of development. Muscle fibers are developed in connection with the tentacles and the distal region of the body, which is retractile. In *Loxosoma* the sexes are separate. The gonads, consisting of a pair of ovaries or testes, lie in the ventral region and open by a common duct. In the development there is a free-swimming *trochophorelike larva* which undergoes a metamorphosis to become the attached adult.

CHAPTER 13

MINOR ANIMAL PHYLA: BRYOZOA, PHORONIDA, BRACHIOPODA, SIPUNCULOIDEA, PRIAPULOIDEA, ECHIUROIDEA, AND CHÆTOGNATHA

The animal groups described in this chapter have been variously classified, and opinion concerning them still differs. One of the older classifications included all of them in a Phylum Vermes, meaning "worms"; but this arrangement now seems unsatisfactory. The classification here chosen, which makes each of these groups a small phylum, appeals to an increasing number of zoölogists.

The Phylum Bryozoa

The Bryozoa, or "moss animals," are attached forms that develop extensive colonies in most species. They have a superficial resemblance to cœlenterates, such as the hydroids and corals, and were so classified until their higher organization was recognized. Typically, there is a

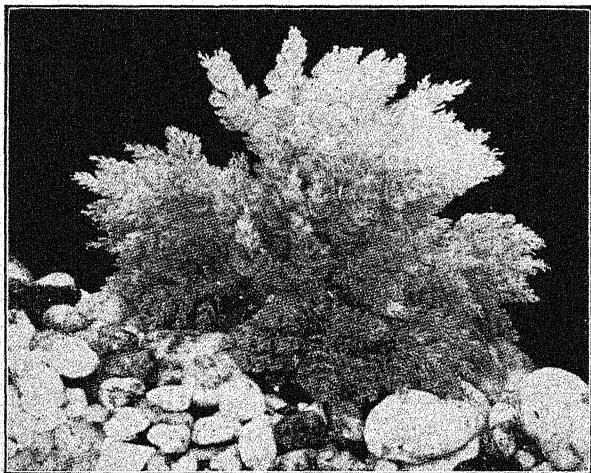


FIG. 286. A colony of *Bugula turrita*.

(From R. C. Osburn, 1910, Bulletin U. S. Bureau Fisheries, vol. 30.)

horseshoe-shaped lophophore, or ciliated ridge, surrounding the mouth and bearing many tentacles. The anus lies just outside this lophophore, making the digestive tract U-shaped, an arrangement that is not uncommon in attached animals (*cf.* Figs. 418 and 433, pp. 555 and 590). What can be called the dorsal surface of the bryozoan is, therefore, the

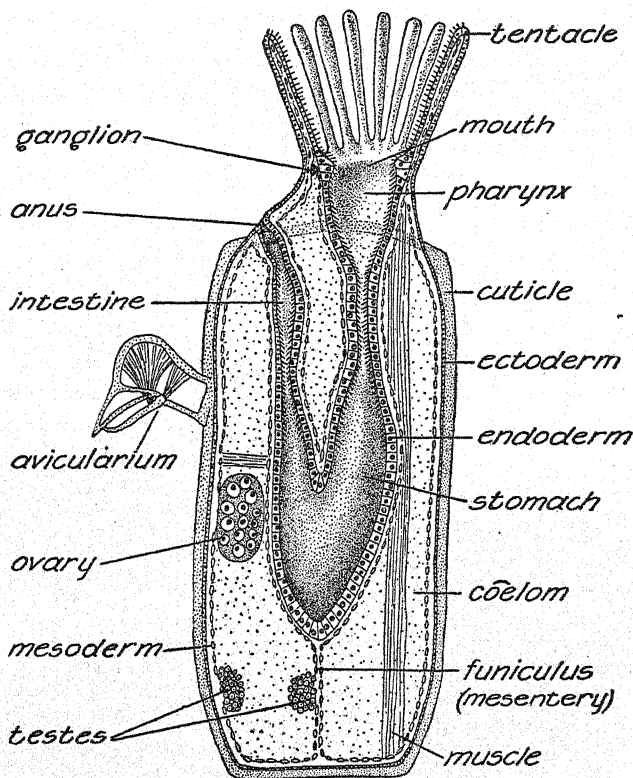


FIG. 287. Zoöid of a bryozoan such as *Bugula*; diagrammatic.

short region between mouth and anus. There are two general types of colonies, one treelike (Fig. 286), and another encrusting (Fig. 288).

The Genus *Bugula*, which is common upon our North Atlantic Coast, is representative of the treelike bryozoan colonies. The individuals of the colony, or *zoöids*, have ciliated tentacles surrounding the mouth (Fig. 287). The anus opens near by but outside the lophophore. Each zoöid can be withdrawn by retractor muscles into its cuplike portion of the cuticular skeleton. In addition to the larger zoöids, specialized zoöids that resemble birds' heads and are called *avicularia* occur upon

the surface of the colony. Their apparent function is to grasp small objects in their beaklike jaws, thus keeping the colony free from the innumerable species of minute animals that establish themselves upon submerged objects in the ocean. In some species certain zooids are specialized to form whiplike appendages, known as *vibracula*. Internally,

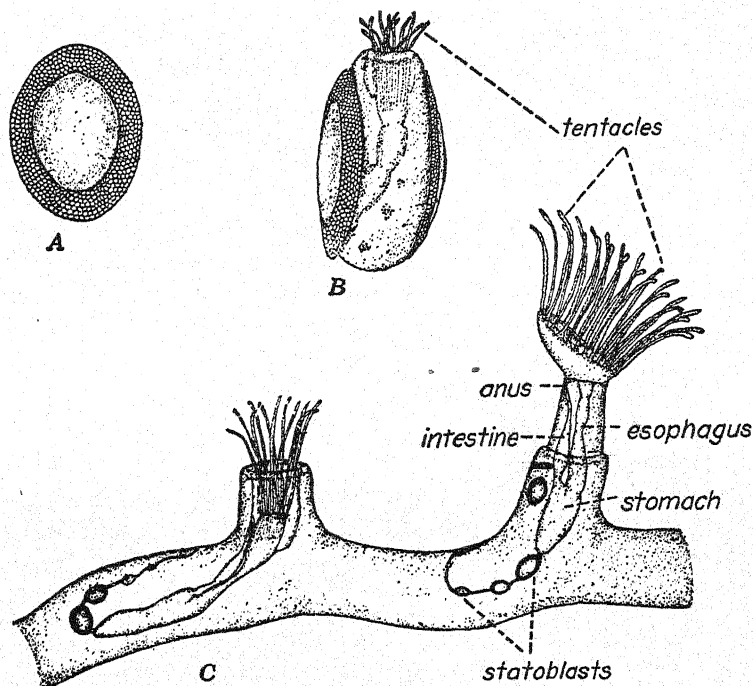


FIG. 288. The fresh-water bryozoan, *Plumatella repens*, and its statoblasts. A, resting statoblast. B, germinating statoblast. C, portion of a mature colony, showing structure and the formation of statoblasts (cf. Fig. 289 C).

(From C. J. D. Brown, 1934, Transactions of Microscopical Society, vol. 53.)

the digestive tract is seen to be U-shaped and is held in position by strands of mesenchyme cells extending across the coelom. Ectoderm, mesoderm, and endoderm are found as in other triploblastic animals. There is a ganglion in the region between mouth and anus with nerves extending to the tentacles, but there are no special sense organs. Neither excretory nor circulatory systems are present. Ovaries and testes occur in the same individual and are formed from cells lining the coelom. Fertilization occurs in the coelom, and early development takes place in a modified region of the zooid, the brood-pouch. The embryo

escapes from the brood-pouch as a free-swimming, *ciliated larva*, resembling a trochophore (cf. Fig. 343, p. 463). At the end of this free life this larva becomes attached and changes into a single zoöid, which forms a new colony by budding. Colonies of the encrusting type are also found among the marine Bryozoa.

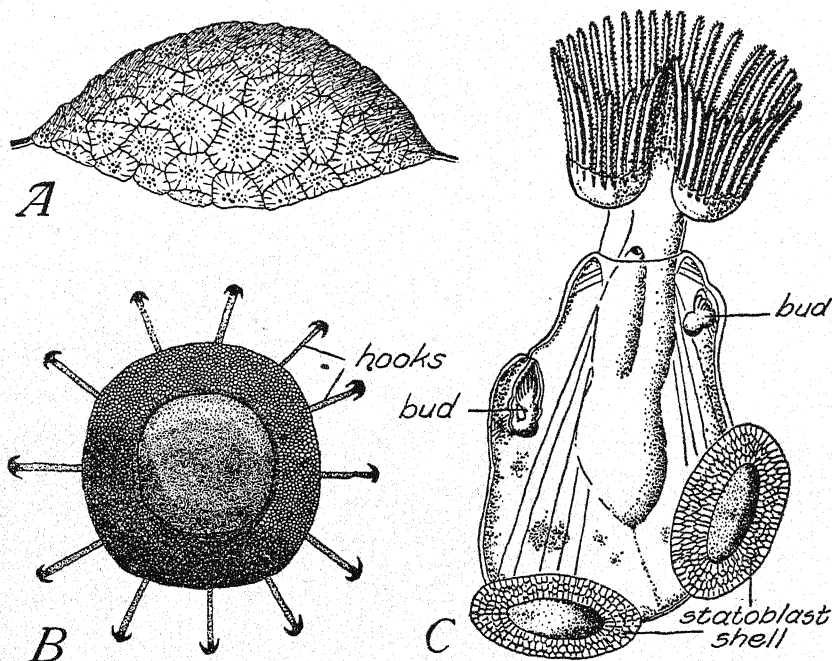


FIG. 289. Fresh-water bryozoans. A, colony of *Pectinatella magnifica*. B, statoblast of same. C, young individual of *Plumatella repens*, recently developed from a statoblast and beginning to bud (cf. Fig. 288 B).

(A, redrawn from C. B. Davenport, 1904, Proceedings U. S. National Museum, vol. 27. B and C, from E. Marcus in P. Schulze, "Biologie der Tiere Deutschlands.")

The colonies of Bryozoa that occur in fresh water are also of two types. Some are branching, like *Plumatella*, which is supported by a skeleton of chitinous material; in others, such as *Pectinatella*, the skeletal secretion takes the form of a large gelatinous mass, on the surface of which the zoöids are found (Fig. 289 A). These fresh-water Bryozoa, like the fresh-water sponges (cf. Fig. 205, p. 308), commonly reproduce by the formation of internal buds, called *statoblasts*, that can resist unfavorable conditions and later develop into new colonies (Figs. 288 and 289).

The Phylum Phoronida

The members of the Phylum *Phoronida* are small marine animals of wormlike shape, found living in tubes which they secrete and into which they can withdraw. The species *Phoronis pacifica* occurs along our Pacific Coast. *Phoronis architecta* is a common species along our Atlantic Coast in the region of North Carolina. Taking *P. architecta* (Fig. 290 A and B) as a representative example, we see that, when the animal is extended, the mouth is located at the exposed end and is surrounded by a whorl of fine tentacles, which somewhat resembles the lophophore of a brachiopod (Fig. 291 A). As in many sessile animals, the anus is located near the mouth but outside the feeding mechanism, which in *Phoronis* is the whorl of tentacles (cf. Fig. 287 and Fig. 418, p. 555). Thus, the digestive tract is U-shaped and what might be called the dorsal surface is the short region between mouth and anus at the exposed extremity. Internally, there is a coelom and a single pair of excretory tubules, or nephridia, leading from this coelom to the outside near the anus. A simple system of blood vessels with pulsatile walls encloses blood with red blood cells. There is a nerve ring around the mouth with a ganglion between mouth and anus, and from this ring, nerves extend to the tentacles and presumably to other parts of the body. There are no special sense organs. In *P. architecta* the sexes seem to be separate, although some species of *Phoronis* are hermaphroditic. The ova and spermatozoa develop in the coelom and leave the body by way of the nephridia. Fertilization occurs externally after the ova and spermatozoa have been discharged. Development of the zygote thus occurs in the open water. A free-swimming, ciliated larva, called the *actinotrocha*, becomes the young *Phoronis* by a striking metamorphosis, during which the digestive tract assumes the U-shape found in the adult and the dorsal region undergoes reduction (Fig. 290 C and D).

The Phylum Brachiopoda

The Brachiopoda, or lamp-shells, are marine animals attached by a stalk and enclosed in bivalve shells somewhat resembling those of clams. It is not surprising that brachiopods were once classified as Mollusca. However, the valves are paired dorso-ventrally, not laterally as in a clam, and a brachiopod's body bears no resemblance to that of a mollusk. In the primitive type of brachiopod, represented by the Genus *Lingula*, there is an anus, and the valves of the shell are not hinged

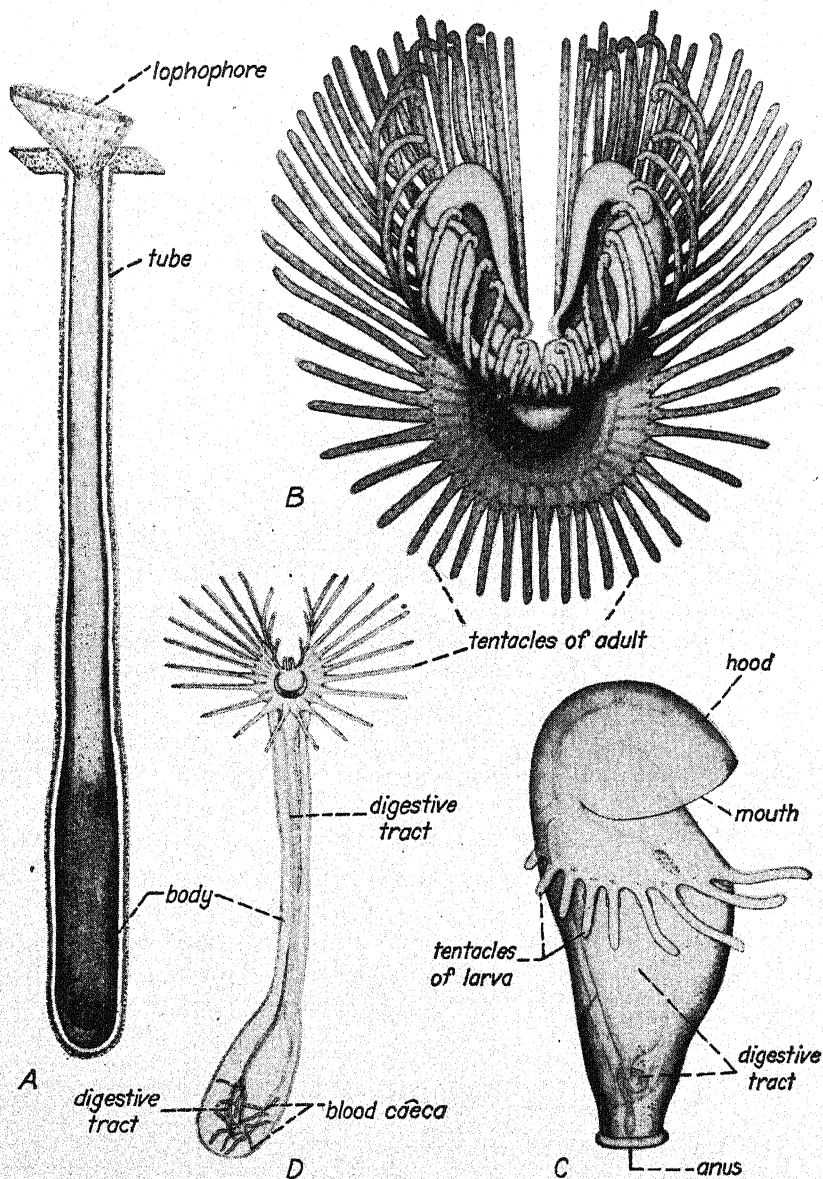


FIG. 290. Structure and development of *Phoronis*. A, *Phoronis architecta* in its tube. B, lophophore of tentacles surrounding the mouth. C, actinotrocha, the free-swimming larva. D, young individual, soon after metamorphosis.

(From R. P. Cowles, 1905, Memoirs National Academy of Sciences, vol. 10.)

(Fig. 291 C). The type represented by the great majority of existing brachiopods, such as the Genus *Terebratulina*, has no anus, and the valves are hinged. The brachiopods are an ancient group. Not more than a hundred and fifty species are known to be now living, but more than twenty-five hundred species have been recorded as fossils, mostly

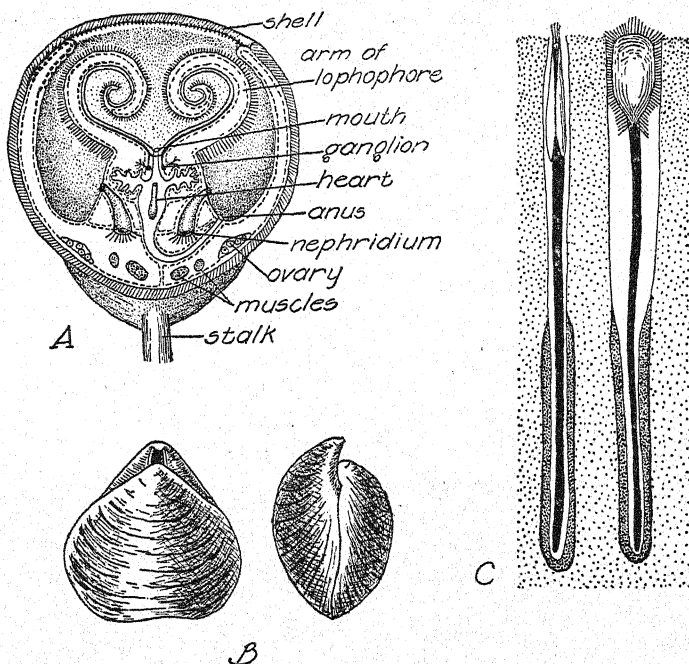


FIG. 291. Brachiopods. A, internal structure from dorsal view; diagrammatic. B, shell of *Rhynchonella*, from dorsal (left) and lateral (right) views. C, *Lingula*, in its tube in the sand; the darker portion of the tube represents sand that is held together by a secretion of the stalk; left, from lateral view; right, from dorsal view.

(A, redrawn from W. Stempel, "Zoölogie im Grundriss," 1926; B, redrawn from A. Lang, "Textbook of Comparative Anatomy," copyright, 1891, by Macmillan and Co., Ltd., printed by permission; C, redrawn after P. François in Y. Delage and E. Hérouard, "Traité de zoologie concrète," 1897.)

from the Palæozoic Age (cf. Fig. 469, p. 646). The existing Genus *Lingula*, which is represented by species in the Cambrian rocks and in later deposits, appears to be the oldest known genus among animals.

In review of the structure found in brachiopods, the shell is horny or calcareous, and the valves, which are opened and closed by muscles, are so placed that the gape is anterior and the hinge is posterior. The dorsal valve is usually the smaller of the two and fits like a lid upon

the ventral (Fig. 291 B). The short stalk, by which the animal is attached to the substratum, extends dorsally through the posterior margin of the ventral valve (Fig. 141 C, p. 222). Internally, the most conspicuous feature is the horseshoe-shaped *lophophore*, which occupies a large part of the cavity enclosed by the valves (Fig. 291 A). This organ suggested the name Brachiopoda, meaning "arm feet." It combines respiratory and sensory functions with the function of food-getting by means of cilia that sweep minute organisms toward the mouth. The digestive system is a simple cavity with digestive glands. The mouth opens into a gullet leading into the stomach and intestine. Only primitive genera, such as *Lingula*, have an anus. There is a contractile heart, but very little is known about the circulatory system. A pair of excretory tubules called nephridia, which also function as reproductive ducts, lead from the coelom to the outer surface. A nerve ring surrounding the gullet gives off numerous branches. The sexes are separate, and the reproductive system consists of two pairs of ovaries or testes, from which the ripe germ cells are discharged into the body cavity (cf. p. 216). They pass to the exterior by way of the nephridia or excretory tubules, and fertilization takes place in the water. Development includes a free-swimming *ciliated larva*.

The Phylum Sipunculoidea

The Sipunculoidea, or geophyorean worms, are a small group of marine animals that burrow in sandy and muddy bottoms or live in tubes which they construct. Although they are sometimes classified with the Annelida or segmented worms, the relationship cannot be clearly established, and it seems better to regard them as a small phylum. *Phascolosoma gouldi*, a species common along our North Atlantic Coast, is a representative example (Fig. 292). The cylindrical body is smaller in diameter toward the anterior end, which can be introverted by means of four retractor muscles. The posterior end tapers to a blunt point. The mouth, which lies at the extreme anterior end, is encircled by small tentacles; the anus lies on the dorsal midline about one-third the length of the worm from the anterior end. Near the anus are the paired openings of the two excretory organs, or nephridia. Internally, the digestive system consists of a slender esophagus and a spirally coiled intestine with a descending portion that extends well toward the posterior end of the body before it turns upon itself to form the ascending portion that reaches to the anus (Fig. 292 B). A spacious coelom contains free cells of several sorts in its coelomic fluid. There are small dorsal and ventral blood vessels, which are pulsatile,

and a circular vessel surrounding the anterior end of the esophagus. Each nephridium is a tubule bent upon itself like a hairpin and attached to the body wall where the two ends of the tube lie close together. The inner end of this tubule opens from the cœlom by a ciliated funnel, and the outer end opens by one of the nephridial openings seen externally. Excretion may occur by passage of fluid into

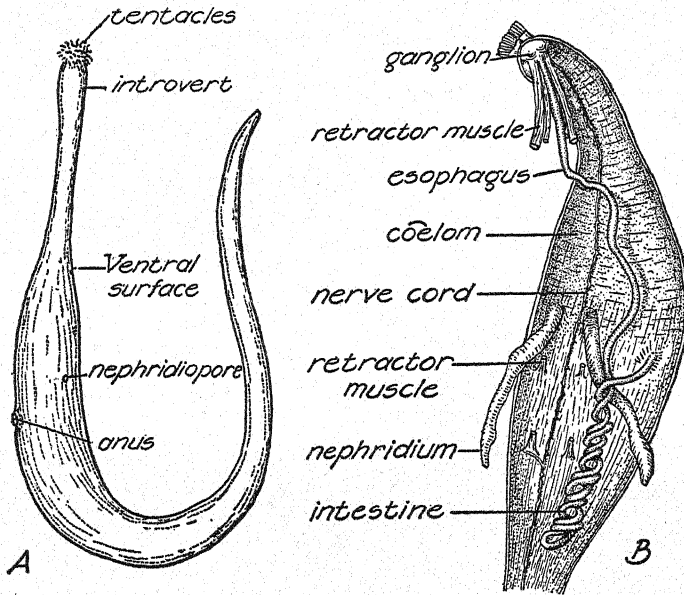


FIG. 292. The sipunculoid worm, *Phascolosoma*. A, extended specimen, from lateral view. B, internal structure; the posterior end of the worm is not shown.

(B, redrawn from J. Leunis, "Synopsis der Thierkunde," 1886.)

the ciliated funnel and through the length of the tubule or by passage of excretions from the cœlomic fluid through the walls of the tubule and so to the outside. The nervous system consists of a nerve ring surrounding the anterior end of the esophagus and a ventral nerve cord from which nerves pass to the body wall. The sexes are separate. The germ cells originate from the walls of the cœlom, float in the cœlomic fluid, and reach the outside by passing through the nephridia, which thus function as reproductive ducts. Fertilization and development take place in the open water. There is a ciliated larval stage, called a *trochophore* because it resembles the larva of this name in mollusks and annelids (cf. Figs. 307 and 343, pp. 425 and 463). This trochophore becomes the miniature adult by a metamorphosis like that

occurring in annelids. During this metamorphosis there are suggestions of metamerism which do not persist in the adult sipunculoid.

The Phyla Priapulioidea and Echiuroidea

To complete the account of lesser phyla, two other wormlike types may be mentioned as sufficiently unlike other groups to justify their classification as two separate phyla.

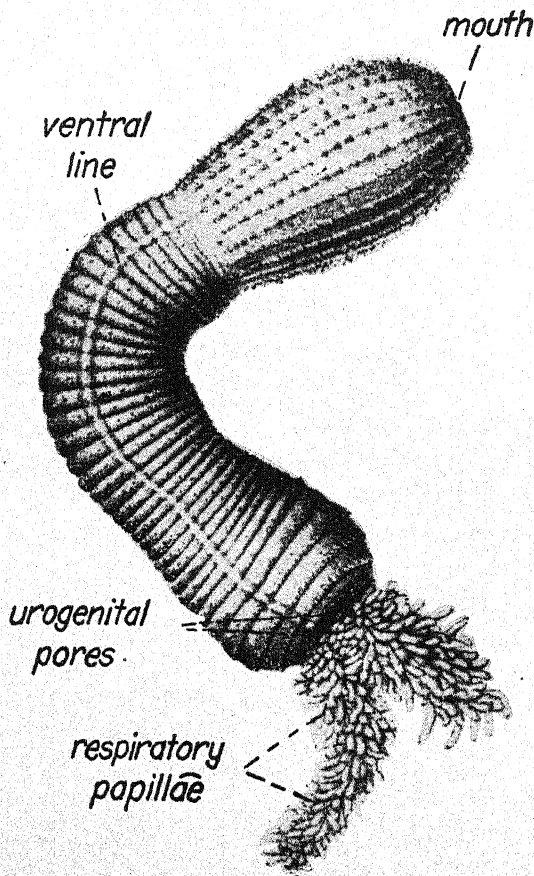


FIG. 293. The priapulid worm, *Priapulus bicaudatus*.
(From F. Baltzer in W. Kükenthal, "Handbuch der Zoologie.")

Members of the Phylum *Priapulioidea*, of which the Genus *Priapulus* (Fig. 293) is representative, are frequently classed with the Sipunculioidea, although their resemblance to sipunculoids is superficial. *Pria-*

pulus is a wormlike marine form, living at moderate depths, and widely distributed outside the tropics.

Members of the Phylum *Echiuroidea*, of which the Genera *Echiurus* and *Thalassema* are representative, are frequently classified with the Annelida, although their structure is quite unlike that of a typical segmented worm such as the clamworm (p. 442) or the common earthworm

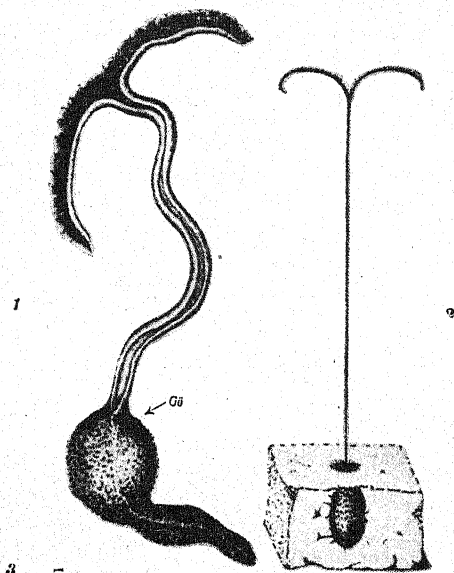


FIG. 294. The echiuroid worm, *Bonellia viridis*. 1, full grown female, from ventral view. 2, female observed in a natural cavity in a stone and with proboscis extended. 3, length of the fully developed male, relative to that of female, as shown in 1. Gö, opening of reproductive duct.

(From F. Baltzer in Kükenthal, "Handbuch der Zoölogie.")

(p. 449). *Thalassema melitta* (cf. Fig. 294) is a familiar species upon our southeastern Atlantic Coast. The adult is commonly found living in the "tests" left vacant by the death of the "sand dollar," *Echinarachnius*, a kind of sea-urchin (Fig. 414 D, p. 551). The proboscis is a distinctive external feature of *Thalassema*, as of other echiuroids. The internal structure presents little resemblance to that of an annelid, and there is no evidence of segmentation. The eggs of *Thalassema* have proved favorable for experimental studies, since they are fertilized and develop in the open water. There is a trochophore stage in the development.

The Phylum Chætognatha

The Phylum *Chætognatha* consists of small marine animals, called "arrow-worms" (Fig. 141 B, p. 222). Their structure sets them apart from other groups, despite the insignificant numbers of species involved. They have been variously classified, but they are clearly animals with a coelom and other features which place them in the evolutionary stem that has culminated in the Chordata (Fig. 150, p. 233). Members of the Genus *Sagitta*, which is representative, are pelagic forms, swimming by means of body movements and horizontal fins (Fig. 295). There are prehensile mouthparts, suggesting the name chætognaths, or "bristle jaws." A relatively large body cavity (cf. p. 216) is divided transversely into three compartments by septa, and there are dorsal and ventral mesenteries. The nervous system consists of a dorsal ganglion, from which nerve cords extend as a circumpharyngeal ring to a ventral ganglion. There are no special excretory or circulatory organs. The animals are hermaphroditic, and the fertilized eggs develop into miniature adults without a ciliated larval stage.

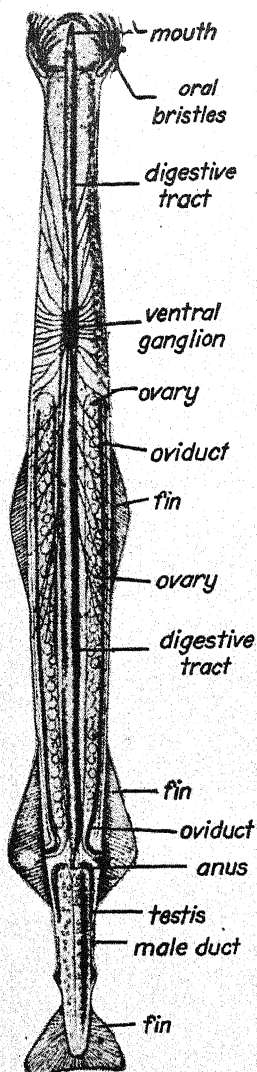


FIG. 295. The chætognath, *Sagitta hexaptera*, in ventral view.

(From H. E. Ziegler, "Zoölogisches Wörterbuch," 1907.)

Shizocœla and Enterocœla

Reference to the table of classification (Fig. 135, p. 215) will show that, except for the Chætognatha, all the animal types described in this chapter are grouped as Schizocœla; they are forms with a true coelom (Eucœlomata), but this coelom originates, typically, as a cleft in the mesoderm (cf. Schizocœla), and not as pouchlike outgrowths from the gut cavity of the embryo (cf. Enterocœla). The other phyla included in this Subdivision Schizocœla (Mollusca, Annelida, and Arthropoda) remain to be considered in subsequent chapters. It will be recalled

that in the Acelomata (Platyhelminthes and Nemertinea) the body is triploblastic, or three-layered, with ectoderm, mesoderm, and endoderm, but without a body cavity of any sort; and that in the Pseudocœlomata (Aschelminthes, Acanthocephala, and Entoprocta) the animal is again three-layered but exhibits a more or less extensive cavity which may be called a "body cavity," but not a true cœlom, as the term is used in this text (*cf.* p. 216). According to such a definition, the cœlom is typically a cavity in the mesoderm, lined by peritoneum and producing the germ cells from this peritoneum or from near-by cells. Associated with the cœlom are tubular excretory organs, the nephridia, which open from it by ciliated funnels and lead to the outer surface, and which may also function as the reproductive ducts. If there are special reproductive ducts leading from cœlom to exterior, as do the nephridia, these ducts are usually regarded as derived from specialized nephridia. In correlation with these features the body and gut walls of cœlomite animals commonly exhibit a well-developed musculature. Although there are exceptions to these structural relationships, this seems to be the fundamental pattern, which has been variously modified during the evolution of the phyla concerned. In the Schizocœla (Fig. 135, p. 215) the cœlom arises, typically, from a cleft in the mesoderm during the early stages of development. In the Enterocœla it arises from pouches growing out of the embryonic gut cavity. Thus, in the Chaetognatha the cœlom originates from the embryonic gut, and for this reason the chaetognaths are classified as Enterocœla. Further consideration of the cœlom as a landmark of comparative anatomy appears in subsequent chapters as the cœlom is described in other phyla.

CHAPTER 14

THE MOLLUSCA

The Mollusca may be defined as bilateral, non-metameric, triploblastic, coelomate animals, with a dorsal calcareous exoskeleton, with a body divided into head, foot, and visceral regions, and with a single pair of nephridia. A characteristic structure called the mantle encloses the most of the external organs except in certain specialized members of the phylum. The word mollusk is derived from the Latin "molluscum," meaning a soft-bodied animal. The phylum is divided into the Class *Amphineura*, or armadillo snails and certain other forms; the Class *Gastropoda*, of which the snails are representative; the Class *Scaphopoda*, a small group of unfamiliar animals sometimes called "tooth-shells"; the Class *Pelecypoda*, or clams, mussels, and oysters; and the Class *Cephalopoda*, or squids, cuttle-fishes, devil-fishes, and nautili.

Typically, the mollusks are free-living animals that creep or burrow and are provided with a protective shell into which they can withdraw, although such mollusks as the cephalopods are modified for a free-swimming life. In the ocean, mollusks are abundant in shallow waters but not at great depths. The primitive habitat seems to have been the ocean, but there are many species of pelecypods and gastropods in fresh water, and gastropods such as snails and slugs are also common on land. The more representative types were correctly classified as Mollusca by Aristotle, Linnæus, and Cuvier, but the early classifications included many animals that have since been distributed to other phyla. Many different kinds of mollusks are used as food, and many molluscan shells have commercial importance. Having shells, the mollusks have left an extensive record as fossils. This chapter emphasizes the fresh-water mussel as an animal to be compared with the frog, the hydra, the planarian, and the earthworm and presents a survey of the phylum.

The Pelecypoda

The Fresh-water Mussel: General Structure and Activities. The account that follows is applicable to any of the more common species

of fresh-water mussels, although it is intended particularly for species of the Genus *Lampsilis*. The *valves* of the *shell* are connected by a *hinge* or ligament (Fig. 296). The domelike part of each valve, called the *umbo* (plural *umbones*), is the oldest portion as shown by the lines or *rings of growth* that extend from the umbo outward and mark the successive outlines of the shell margin. The orientation is such that the hinge is dorsal, and the anterior and posterior margins of the valves may be distinguished by the greater extent of the posterior

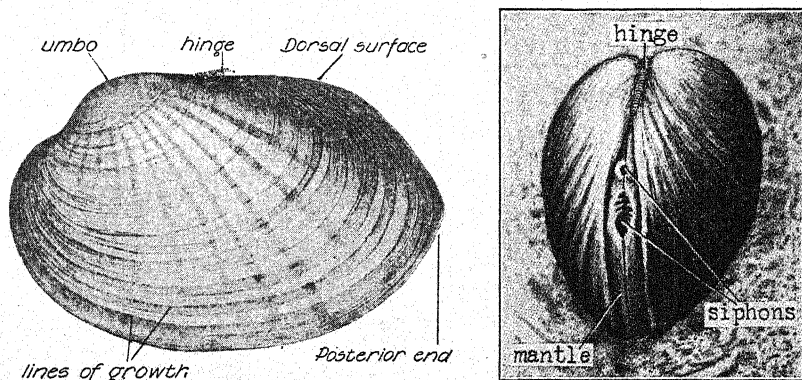


FIG. 296. *Left*, the shell of a fresh-water mussel, *Lampsilis ligamentina*. *Right*, a mussel in its natural position partially embedded in the bottom, from posterior view.

(*Left*, from R. E. Coker, 1917-18, Bulletin U. S. Bureau Fisheries, vol. 36. *Right*, from R. E. Coker, A. F. Shira, H. W. Clark, and A. D. Howard, 1919-20, Bulletin U. S. Bureau Fisheries, vol. 37.)

one. When the mussel is expanded, as in feeding or locomotion, the valves gape slightly along their ventral margins, but this space is filled by the edge of the so-called *mantle* (Fig. 296). Before the shell is removed, nothing more can be seen of the living parts, except as the *foot* is thrust from between the antero-ventral margins of the valves or the tubelike *siphons* are extended slightly in the postero-dorsal region.

After the shell has been removed, it is seen that each valve fits closely over the underlying parts and is firmly attached to the ends of the two *adductor muscles*, which close the valves, and to the *retractor* and *protractor muscles* of the foot (Fig. 297). The valve is also attached firmly along a line parallel to its margin, where the muscle fibers that retract the edge of the mantle are inserted. The *visceral mass*, which contains the internal organs, makes up the dorsal region of the body. From this mass the mantle extends ventrally on each side beneath the shell and encloses the so-called *mantle cavity*, into which the foot and

gills protrude. The mantle cavity is really part of the outer surface of the animal, although it seems internal. If the mantle of one side is removed, the mantle cavity and its organs are fully exposed (Fig. 297). The siphons are now seen to be formed by the fitting together and local differentiation of the right and left margins of the mantle. Four plate-like *gills*, which are attached along a line from a point between the siphons to a point opposite the umbones of the valves, hang freely in

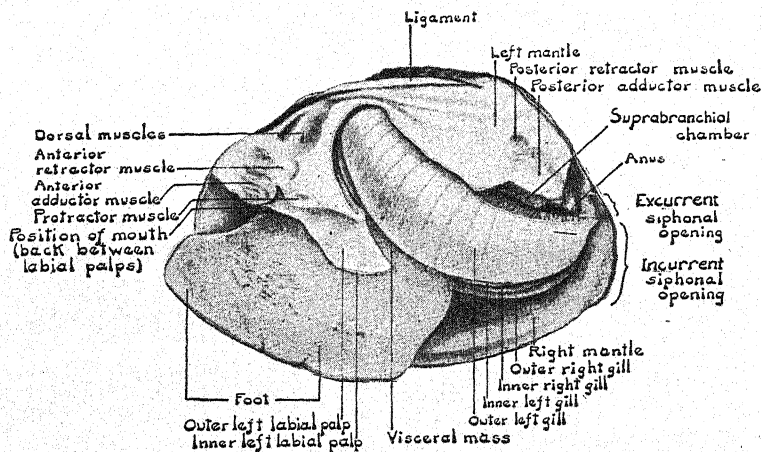


FIG. 297. Organs of the mantle cavity of a fresh-water mussel, *Symphynota complanata*; the left valve of the shell and left half of the mantle have been removed. In this species the entire outer gill on each side is modified as a brood-pouch.

(From G. Lefevre and W. C. Curtis, 1910, Bulletin U. S. Bureau Fisheries, vol. 30.)

the angle between the visceral mass and mantle, a pair on each side. Anterior to the gills are the *palps*, which are paired like the gills. The *mouth* lies in the angle between the foot and the anterior adductor muscle, and the palps of each side are connected in the mouth region by ridges that extend transversely like an upper and a lower lip.

When the animal is embedded in the bottom, it usually lies with the median plane vertical and only the postero-dorsal margin of the valves visible (Figs. 296 and 303). The valves are held slightly gaping by the springlike action of the hinge and are drawn together by the adductor muscles. If they are gaping, as when the mussel is fully expanded, the margins of the mantle appear as a fleshy mass. When the siphons are open, a gentle current of water is passing continually into the ventral or *incurrent siphon* and out the dorsal or *excurrent siphon*. During locomotion, the foot is thrust forward, expanded at

its free end or turned so that it takes a clumsy hold upon the bottom, and the mussel is drawn along when the foot contracts. When the animal is at rest and embedded in the bottom, the foot may be extended into the mud or withdrawn into the mantle cavity.

Structures and Functions Related to Metabolism and Irritability. The water that enters the mantle cavity by the incurrent siphon is drawn through the *ostia*, or minute ciliated openings on the surfaces of the gills, into the *water tubes*, which are vertical passages leading to the four *suprabranchial chambers*, one above each gill. These supra-

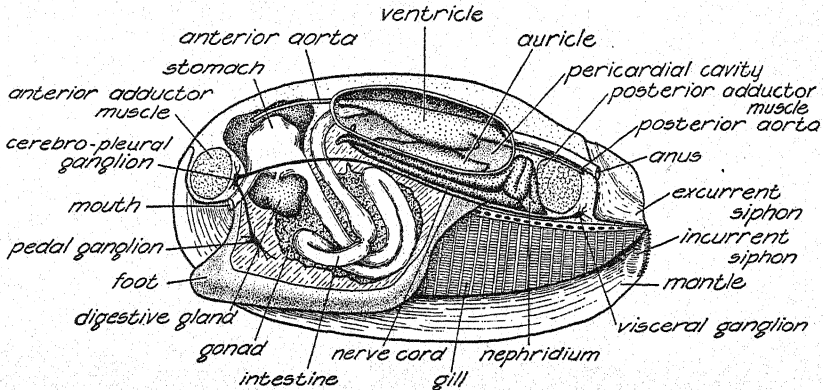


FIG. 298. Internal structure of the mussel, *Anodonta*; semidiagrammatic.

branchial chambers unite beneath the posterior adductor muscle and are continuous with a region of the mantle cavity known as the *excurrent chamber*, or cloaca, which opens externally by way of the excurrent siphon. The current of water that flows through the gills brings the animal its food as well as oxygen. The gill surfaces with their ostia, through which the water is constantly flowing, function as a sieve that strains out all but the very minute particles suspended in the water. In addition the gill and mantle surfaces secrete mucus, in which these particles become entangled. Thus, the food of the mussel, which consists of minute organisms and organic debris, is caught by the gills and mantle. This food is then transported by ciliary action, which conveys the mucus and food particles along definite paths to the space between the palps of each side and thence to the mouth. A similar transportation of particles and mucus occurs in the mouth of the frog. Among the Mollusca this method of feeding is unique for the pelecypods, although a similar process occurs in some other animals, notably the tunicates (*cf.* p. 591 and Fig. 433, p. 590). In other classes of the Mollusca, the food consists typically of animal or plant material, which

is seized and devoured or torn away by a rasplike tongue called the radula.

The *digestive system* is composed of a short *esophagus* leading to a *stomach*, into which paired *digestive glands* open (Fig. 298). The *intestine*, which is coiled in the visceral mass dorsal to the foot, leads to the *rectum*, which reaches the *anus* after traversing a small cavity, the *cœlom*, or pericardial cavity (Figs. 298 and 299). Within the rectum is a longitudinal fold, the *typhlosole*, which presumably serves to increase the surface available for absorption of food. The anus opens, dorsal to the posterior adductor muscle, into the excurrent chamber of the mantle cavity near the excurrent siphon. Feeding as it does upon organic debris and microorganisms, the mussel needs no mechanism for the reduction of its food to a pasty mass of small particles. The fluid from the digestive glands thus functions in what may be compared with the final stages of digestion in many animals. It is presumed that *digestion* and *absorption* begin in the stomach and are completed in the intestine. At times the stomach contains a gelatinous rod, called the *crystalline style*, and similar rods are found in many pelecypods. The function of these rods is obscure; they may be related to food storage.

The *circulatory system* includes a *heart* composed of right and left *auricles* that enter a single *ventricle*, which is wrapped about the rectum where it passes through the cœlom. Because it thus contains the heart, the cœlom of the mussel is also called the *pericardial cavity*. The circulatory system differs from that of the vertebrate in that some of the vessels connecting the arteries and veins do not have a continuous cellular lining and are, therefore, *sinuses* rather than capillaries. The food and oxygen carried in the blood of such a system can pass directly into the intercellular spaces; they are not restricted to diffusion through the walls of the blood vessels. In its circulation the blood passes from the ventricle into *anterior* and *posterior aortæ*, which lead to all parts of the body with the exception of the nephridia and gills (Fig. 299). From the regions thus supplied, with the exception of the mantle, the blood is carried to the nephridia and thence to the gills. From the mantle and gills on each side the blood returns to the auricle of that side; the right and left auricles open into the ventricle. The *excretory system* consists of a pair of *nephridia*, which are tubes leading from the anterior end of the cœlom to their external openings in the supra-branchial chambers of the inner gills. Each nephridium is folded upon itself and is differentiated into glandular and bladderlike portions (cf. Figs. 298 and 299). Manifestly, the structure is such that excretions in solution within the cœlomic, or pericardial, cavity may enter the

tubule; or the excretions may be passed into the tubule by the cells lining the glandular portion of the nephridium and then to the outside. The exact manner of the process is not known.

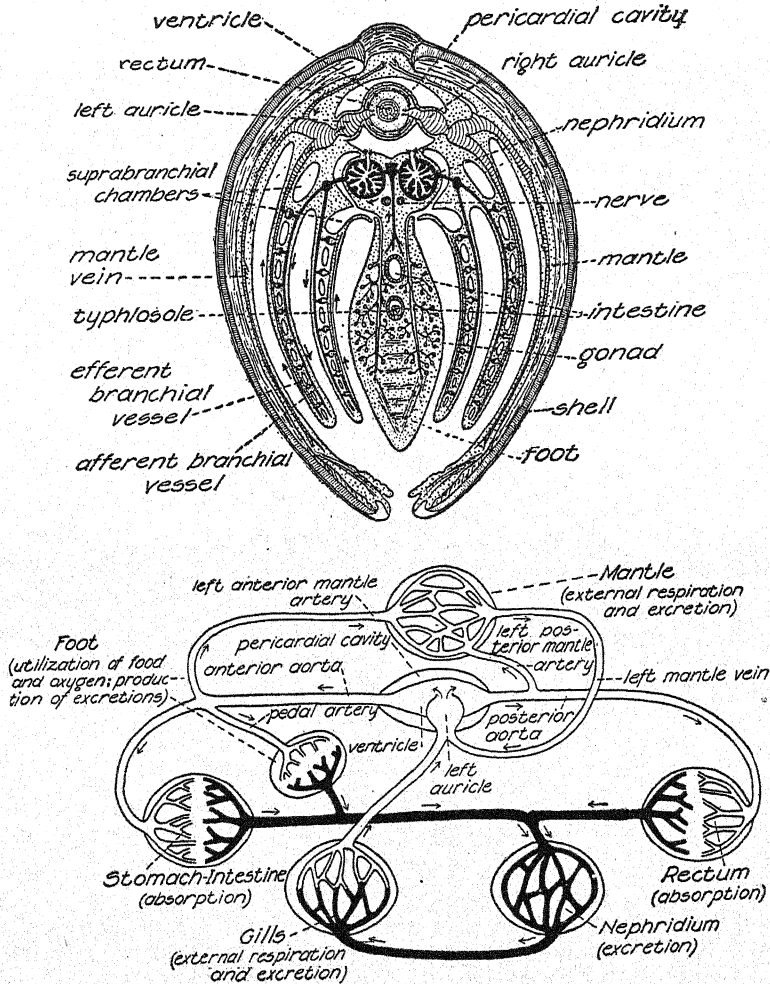


FIG. 299. Circulatory system of *Anodonta*. Above, diagrammatic cross section of the mussel, showing the heart and principal blood vessels. Below, diagram showing course of the circulation.

(Upper figure from W. Stempel, "Zoölogie im Grundriss," 1926.)

The *nervous system* consists of a pair of *cerebral ganglia*, one on each side of the mouth, a pair of *pedal ganglia* in the foot, and a pair of *visceral ganglia* ventral to the posterior adductor muscle (Fig. 300).

These pairs of ganglia are united by commissures between ganglia of the same pair and by the cerebro-pedal and cerebro-visceral connectives. *Nerves* extend from the ganglia to the sensory surfaces of the

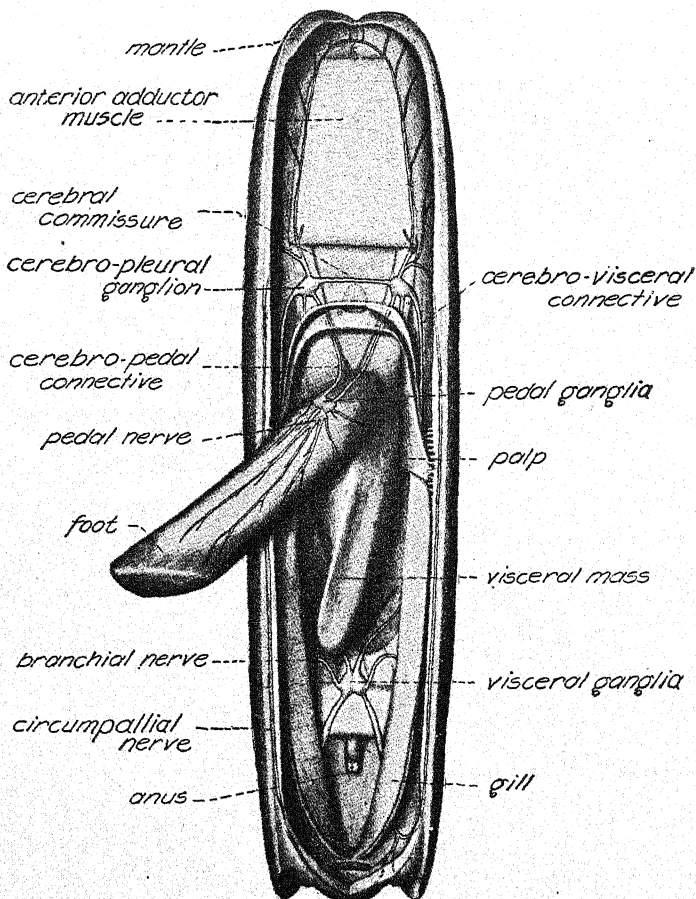


FIG. 300. Nervous system of the razor-shell clam, *Ensis directus*, ventral view. The relationships of ganglia and nerves are similar to those in the fresh-water mussels (cf. Fig. 298).

(From G. A. Drew, 1908, Jour. Experimental Zoölogy, vol. 5.)

body and to the muscles. The *sense organs* include tactile parts, such as the papillæ of the siphons, which are also sensitive to light; the osphradia, two areas of sensory epithelium located near the visceral ganglia, which function as chemoreceptors; and a pair of organs of equilibrium, the statocysts, which are located in the foot near the pedal ganglia (cf. Fig. 301).

. So far as the activities related to *metabolism* and *irritability* have been studied in the mussel, they resemble those of other animals with a comparable degree of complexity. Mussels are sluggish animals with a low rate of metabolism and hence a relatively simple sensory-neuro-muscular mechanism.

The Reproductive Organs, Reproduction, and Development. In most fresh-water mussels the sexes are separate. The *ovaries* and *testes* are embedded in the visceral mass, among the coils of the intestine, with ducts opening into the suprabranchial chambers near the openings of the nephridia (Fig. 298). The spermatozoa reach the external water through the excurrent siphon. They may then enter a female through the incurrent siphon, pass through the ostia, and reach the suprabranchial chambers into which the ova are discharged and where fertilization occurs. In *Lampsilis* the fertilized eggs are passed to the suprabranchial chambers of each outer gill and fall into the water tubes of these gills, which are modified during the breeding season as brood-pouches (Fig. 302).

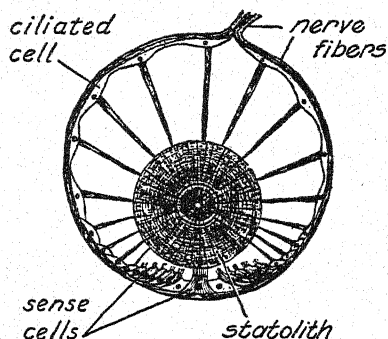


FIG. 301. Statocyst of the gastropod *Pterotrachea*.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

Each zygote develops within the brood-pouch into a stage called the *glochidium* and remains in this stage until discharged through the excurrent siphon. When so discharged, a glochidium can only lie upon the bottom, since it has no power of locomotion and dies within a few days unless it happens to come into contact with a fish (Fig. 303). In this event the glochidium clamps its valves upon the edge of the fish's fin or upon a gill filament and becomes overgrown by the epidermis of the fish, upon which the glochidium is now parasitic (Figs. 303 and 304). When the organs are sufficiently developed, the young mussel leaves the fish and begins an independent life upon the bottom. The glochidia of some genera, such as *Lampsilis*, are parasitic upon the gills of fishes; others, such as the glochidia of *Symphynota*, are parasites upon the fins (Fig. 304). Like the majority of parasitic animals, glochidia are specialists in the sense that they can live upon only one species or a few closely related species of hosts. Upon leaving the fish, the young mussel grows rapidly if it finds a favorable environment upon the bottom, and the shell outline of the adult is soon apparent, al-

though the outline of the glochidial shell remains at the umbo until it is worn away (Fig. 305).

Such a mode of development is exceptional among the Pelecypoda. In the great majority of species the ova and spermatozoa are dis-

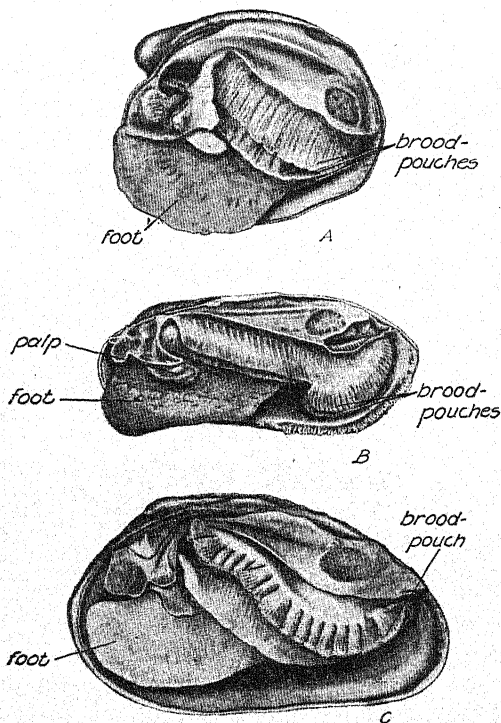


FIG. 302. Modifications of gills in gravid females of fresh-water mussels to form brood-pouches. *A*, *Quadrula ebena*, in which the entire inner and outer gills form brood-pouches. *B*, *Lampsilis recta*, in which the posterior half of each outer gill is modified to form a brood-pouch. *C*, *Ptychobranchus phaseolus*, in which the ventral half of each outer gill forms a brood-pouch (cf. Fig. 297).

(From G. Lefevre and W. C. Curtis, 1910, Bulletin U. S. Bureau Fisheries, vol. 30.)

charged from the excurrent siphon, and fertilization occurs in the open water. The fertilized egg then develops into a ciliated larva, the *veliger*, somewhat resembling the trochophore of annelids (Fig. 343, p. 463), which settles to the bottom as it assumes the characteristics of the adult. The American oyster develops in this manner before it settles and becomes attached (Figs. 307 and 308).

As a group the pelecypods are predominantly of separate sexes. A

few species, however, are hermaphroditic. In some of these it has been observed that the individual may at first be of one sex and later change to the opposite sex. Apparently, there is a cycle peculiar to each species. The gastropod mollusks exhibit many more such examples. These observations are of interest, although their relation to the problem of sex determination in other animals is not yet apparent

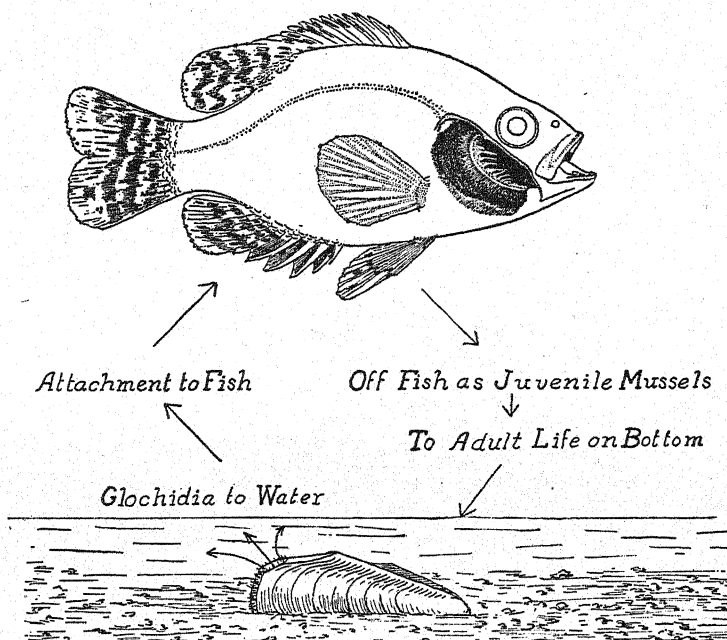


FIG. 303. Life-cycle of a fresh-water mussel. The gill covering, or operculum, of the fish has been removed, showing the gills heavily infected with glochidia.

(cf. p. 203). A few pelecypods are viviparous. In the fresh-water Genus *Sphærium*, for example, the eggs are fertilized and develop to miniature adults in brood-pouches formed in the water tubes of the inner gills. In *Nucula delphinodonta* a brood-pouch, which is formed by secretion, is attached to the outer surface of the shell.

Economic Importance. The fresh-water mussels acquired economic importance in the United States when it was found in 1891 that the shells of many species could be used for the manufacture of pearl buttons, which up to that time had been extensively produced only from the shells of certain marine forms. As the upper Mississippi River and its eastern tributaries then contained the greatest wealth of fresh-water mussels that has ever been found in any part of the world,

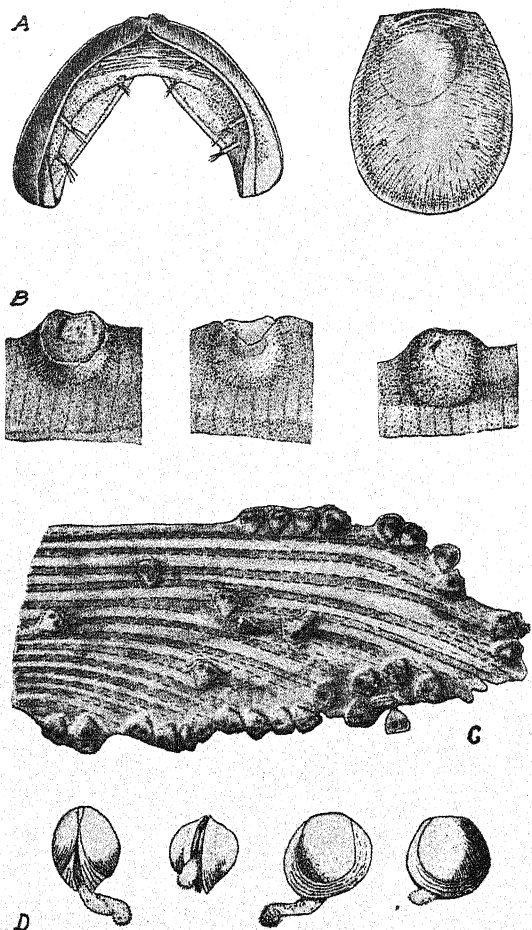


FIG. 304. The development of fresh-water mussels. *A*, glochidium of *Lampsilis*: left, from posterior view; right, from lateral view. *B*, successive stages in the embedding of a glochidium of *Lampsilis* upon a gill filament of a fish. *C*, fin of a fish with a number of embedded glochidia of *Symphynota*. *D*, juvenile *Lampsilis*, crawling upon the bottom after leaving the fish and showing the persistent glochidial shell.

(From G. Lefevre and W. C. Curtis, 1910, Bulletin U. S. Bureau Fisheries, vol. 30.)

the fishing was rapidly extended (Fig. 306). At first the supply seemed inexhaustible, but within a dozen years the great beds were so depleted that operations were extended to more remote localities. It is now evident that this supply of raw material for the American button industry is doomed except in so far as methods of artificial propagation can be applied.

The United States Fisheries Service has long been concerned with this matter and early developed methods by which fish could be artificially infected with glochidia and made to carry much larger numbers than they ever carry in nature. The habits of the juvenile stages and the growth stages of the adult mussels were also investigated with reference to propagation. Mussels, such as the "nigger-head," *Quadrula ebena*, which furnished the most-prized shells in the early days of

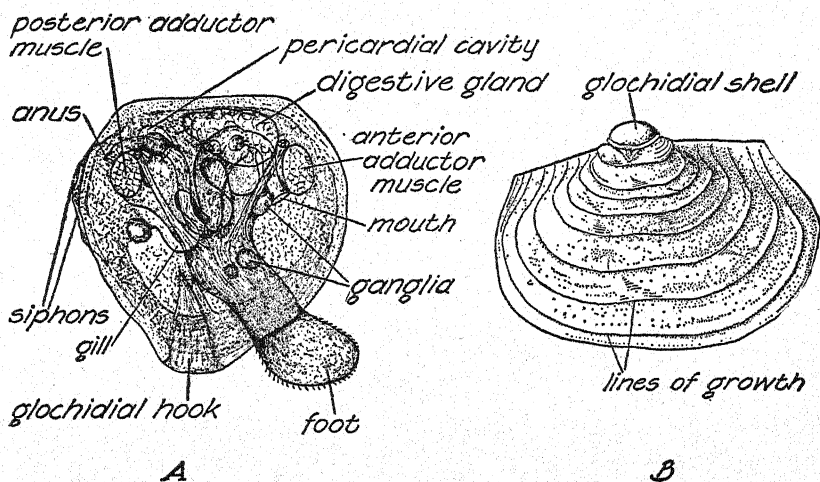


FIG. 305. Juvenile stages of fresh-water mussels. A, *Symphynota*, shortly after leaving the fish. B, *Anodonta*, seven weeks after leaving fish.

(A, from G. Lefevre and W. C. Curtis, *op. cit.*; B, from K. Herbers, 1913, *Zeitschrift für wissenschaftliche Zoologie*, vol. 8.)

the American button industry, have a slow growth rate. Large shells may be as much as 25 years old. On the other hand, good button shells are produced by some species of *Lampsilis* in 4 or 5 years. Farther south there are species that grow almost continuously without the period of winter rest and that live in bodies of water such as irrigation ditches and storage ponds. By taking advantage of all this knowledge, it is probable that mussels will eventually be grown under controlled conditions and a valuable natural resource preserved. The pearl button holds its own commercially because no artificial material has yet been produced that will so long retain an attractive appearance and resist the stress of laundering.

Pearls are found in fresh-water mussels and in many other pelecypods. A pearl is secreted by the mantle in the same manner as the pearly lining of the shell and, unless it has been displaced, lies in a

pocket between the mantle and the shell (Fig. 310). The secretion is apparently initiated by some foreign body coming between the shell and mantle. Pearls that occur in fresh-water mussels are usually small and imperfect, although some valuable specimens have been found. The irregular ones, called baroques, may be valuable if attractive in appearance. The most important source of pearls has been the pearl oysters of the tropical and subtropical oceans. Production of

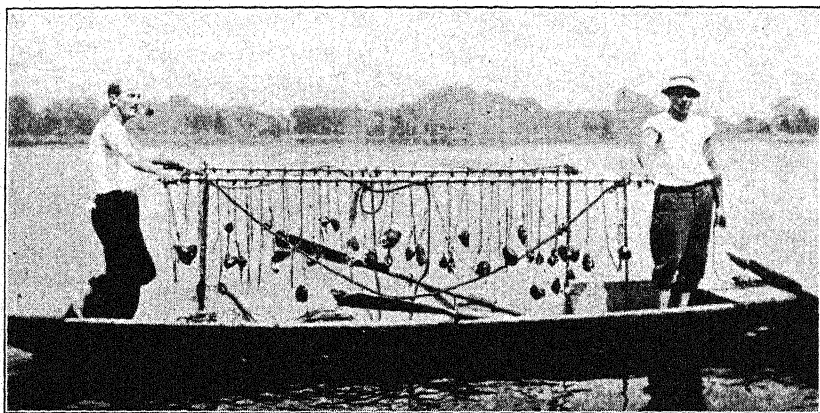


FIG. 306. Mussel fishermen on the Mississippi River with two crow-foot dredges used to catch mussels for the pearl-button industry. The dredge consists of iron bars to which cords with four-pronged hooks are attached at intervals of a few inches. As the dredge is dragged along the bottom, the prongs slip between the slightly gaping valves of the mussel shells, which close tightly in response to this stimulus, so that the animals are torn from their places on the bottom and drawn to the surface.

what are called "cultured," in contrast with "natural," pearls has been perfected by the Japanese, Mikimoto (Fig. 311), and has resulted in the development of an important industry. Cultured pearls are essentially the same as natural pearls, although it is claimed that the two can be distinguished by experts. The formation of such a pearl is stimulated by introducing a foreign body between the mantle and shell. In the Mikimoto establishments the oysters are collected by divers, brought to the near-by laboratory for introduction of the foreign body, and then kept for several years in wire cages suspended from rafts. During this period they are examined repeatedly, and the outer surface of the shell is scrubbed to remove the plant and animal growths that accumulate on such submerged objects and may check the growth of the oyster. After 5 or 6 years they are finally opened, and a substantial percentage contain valuable pearls.

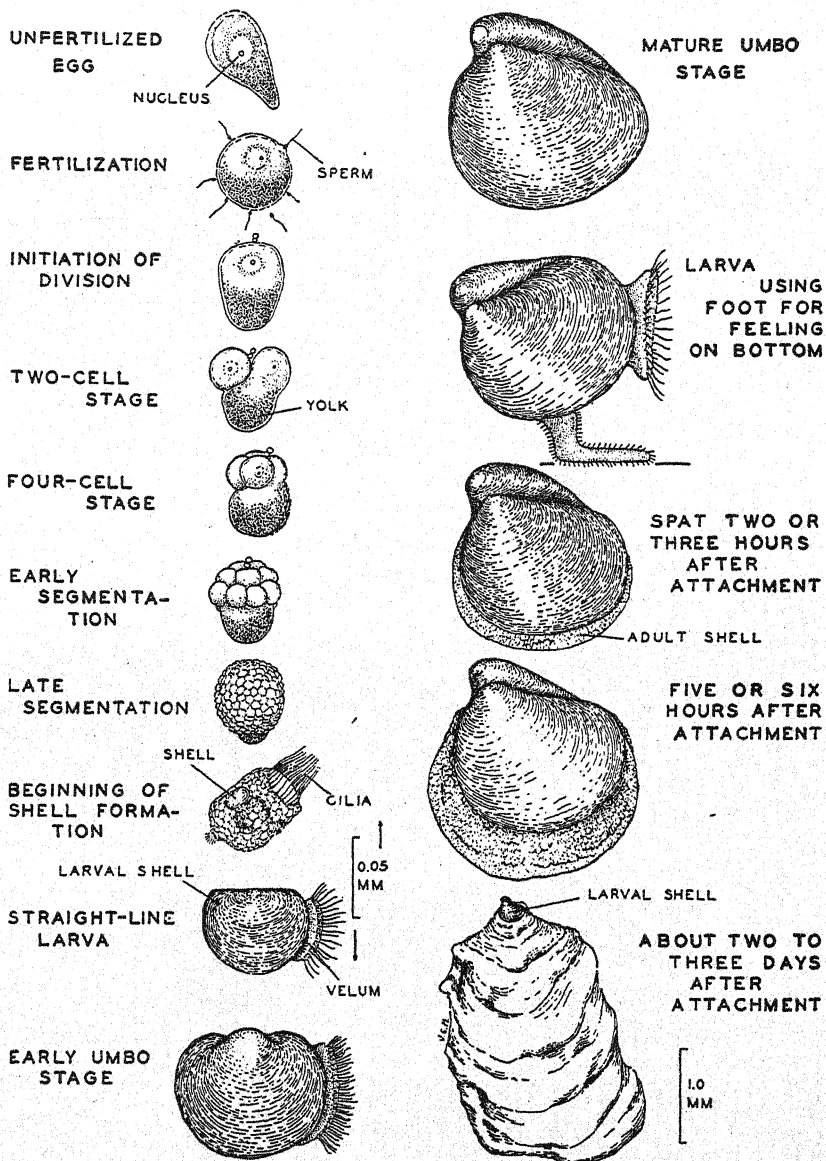


FIG. 307. Development of the oyster.

(From C. L. Newcombe and R. W. Menzel, Contribution No. 22, Virginia Fisheries Laboratory, 1945.)

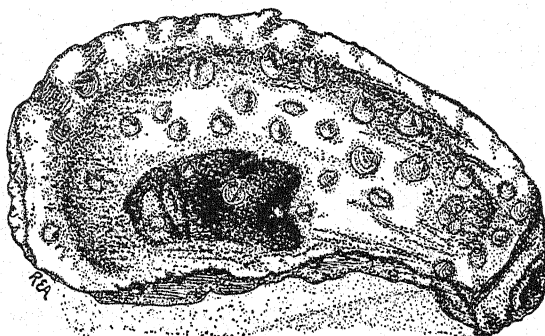


FIG. 308. Young oysters, called "spat," attached to a dead oyster shell, as they are often found in nature (*cf.* attached stage shown in Fig. 307).

(From Newcombe and Menzel, *op. cit.*)

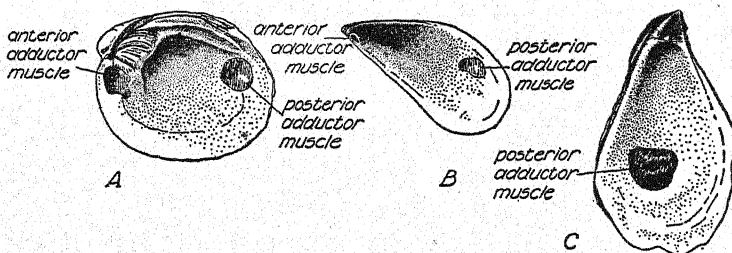


FIG. 309. Shells of bivalve mollusks, showing attachments and relative sizes of the anterior and posterior adductor muscles. *A*, a fresh-water mussel. *B*, the salt-water mussel, *Mytilus*. *C*, the oyster, *Ostrea*.

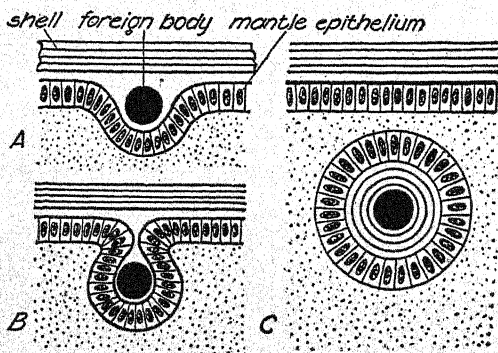


FIG. 310. Formation of a pearl around a foreign body between the shell and mantle; diagrammatic.

(From F. Haas in H. G. Bronn, "Klassen und Ordnungen des Tier-Reichs.")

Other Pelecypoda. There is great diversity in the superficial appearance of pelecypods, although the bivalved shell can be recognized without difficulty in almost all species. The parts conspicuously modified are the shell and its adductor muscles, the mantle, the foot, and the gills. The primitive type of shell and muscles is one with anterior and



FIG. 311. Pearl-oyster collecting and culture. *Left*, girls diving for pearl oysters at the Mikimoto station, Toba, Japan. *Right*, Mr. Mikimoto, the "pearl king"; in the background, one of the rafts from which many cages containing the oysters are suspended during the period of pearl culture.

posterior adductors equally developed, with the hinge lying between these two muscles and with a shell outline like that of the fresh-water mussel. In this type a line drawn between the centers of the two adductors is approximately parallel with the hinge axis (Fig. 309 A). The type found in the salt-water mussel, *Mytilus*, has the posterior ad-

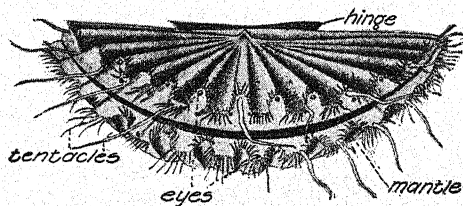


FIG. 312. The scallop, *Pecten jacobæus*; from ventral view.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

ductor larger than the anterior and the line between these muscles at an angle with the hinge axis (Fig. 309 B). In the oyster, *Ostrea*, and the scallop, *Pecten*, there is only one muscle, the posterior adductor, to close the valves (Fig. 309 C). The early stages of the oyster and scallop show anterior as well as posterior adductors; later stages show

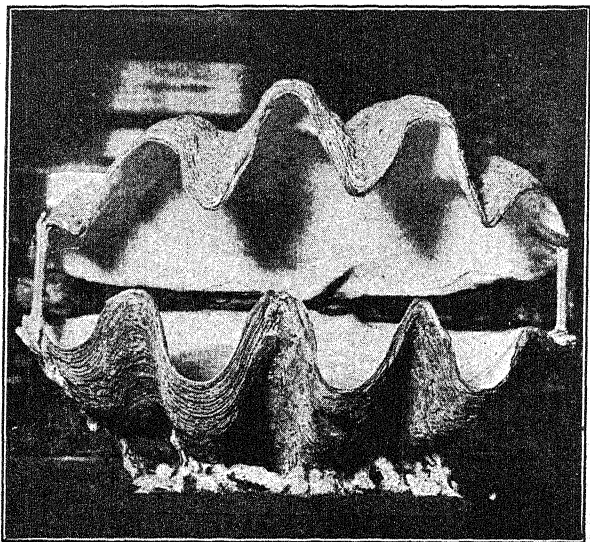


FIG. 313. Shell of the giant clam, *Tridacna gigas*, from the Philippine Islands; the shell may weigh as much as 440 pounds and be over three feet in length.

(Photograph by courtesy of American Museum of Natural History.)

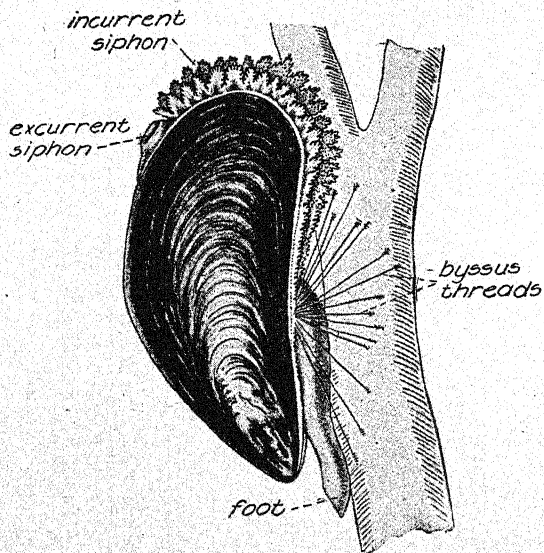


FIG. 314. The salt-water mussel, *Mytilus edulis*, attached by byssus threads.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

the anterior member of the pair disappearing as the line between the two muscles comes to lie at a right angle to the hinge axis.

The shell of a pelecypod may be of light weight, as in the fresh-water mussel *Anodonta*, which crawls upon soft muddy bottoms, and in the scallop *Pecten*, which swims by clapping the valves of its shell together and ejecting a jet of water (Fig. 312). In the oyster and the giant clam the shell is massive (Fig. 313).

The foot may be moderately developed, as in the fresh-water mussels, or absent, as in the adult oyster, or relatively large, as in active burrowers such as the razor-shell clam, *Ensis* (Fig. 300). In the foot of many pelecypods is a gland, called the *byssus*, that secretes threads by which the juvenile stages attach themselves to objects on the bottom. In a few

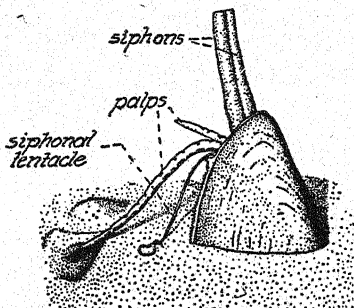


FIG. 315. *Yoldia limatula*, embedded in the bottom and feeding. The palps, which are elongated and specialized, protrude from between the posterior edges of the mantle and extend over the bottom gathering food. The siphonal tentacles are sensory structures arising at the base of the siphons.

(From G. A. Drew, 1901, Quarterly Jour. Microscopical Science, vol. 44.)

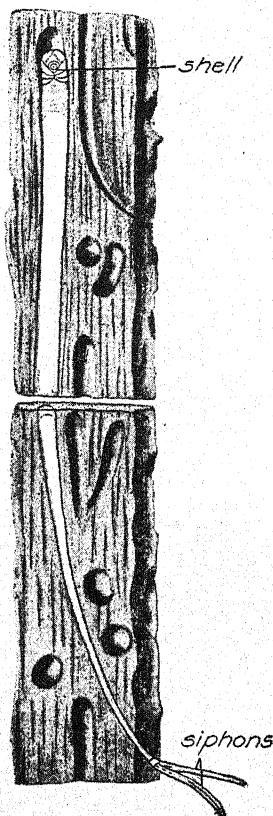


FIG. 316. The shipworm, *Teredo navalis*, in its burrow within a piece of submerged wood; the middle portion of the body is not shown. The siphons are exposed in the water, and the boring mechanism consisting of the modified shell is seen at the inner end of the burrow.

(From W. Stempel, Zoölogie im Grundriss, 1926.)

pelecypods, such as *Mytilus*, the byssus is still functional in the adult animal, and the foot is greatly reduced (Fig. 314).

The siphons of the fresh-water mussel are formed by apposition of the two sides of the mantle and a slight differentiation in this region. Such a form as *Mytilus* has a single fusion of the two sides of the mantle separating the excurrent from the incurrent siphon, which in *Mytilus* is an extensive region marked by fringed edges (Fig. 314). In other genera there is a second fusion, and the siphons appear as a double tube. A clam with siphons of this sort can live buried deeply,

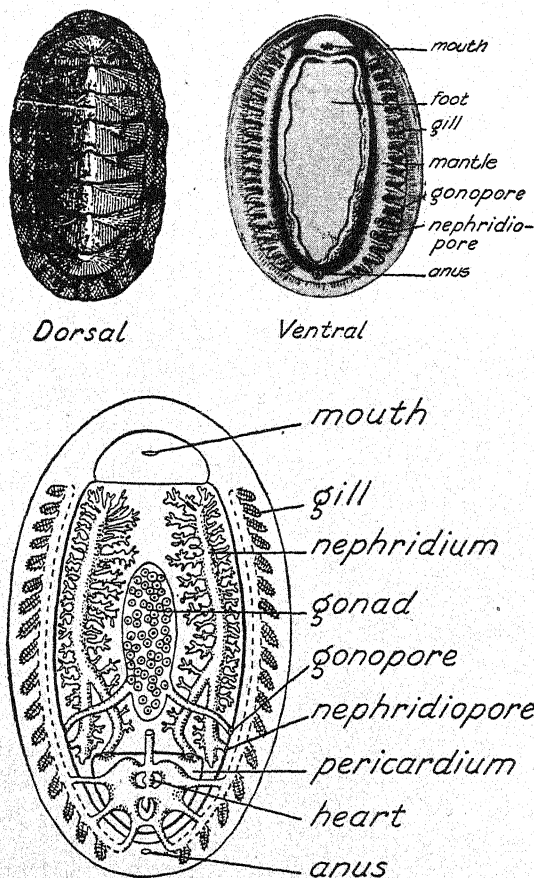


FIG. 317. The amphineuran, *Chiton olivaceus*. Above, external features. Below, internal structure, from ventral view; diagrammatic.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

or can secure food and discharge waste by extending its siphons along the bottom, as does *Cumingia*. Modifications of the gills and palps are less frequent but sometimes extreme, as in *Yoldia* (Fig. 315).

The extremes of external appearance in pelecypods are illustrated by the "shipworm," *Teredo*, and the giant clam, *Tridacna* (Figs. 313 and 316). The shipworm is so called because it infests the planking of wooden vessels, into which it bores, as it does into any submerged wood that is not artificially protected. The animal is wormlike, but the siphons, which protrude posteriorly; and the modified bivalve shell, which is part of the boring mechanism at the anterior end, are marks of its pelecypod nature. In comparison with other mollusks, the members of the Class Pelecypoda are laterally compressed, the shell is bivalved, and the entire organization is modified in relation to a mode of feeding not found in the other classes.

The Amphineura

The most representative type among the Amphineura is the chitons (Fig. 317). These mollusks are not uncommon at the seashore, although the number of species and individuals is insignificant when compared with such a class as the Gastropoda. The *shell* of the chiton consists of eight plates on the dorsal side of the body. In some chitons these plates are covered by an integument. Ventrally there is a creeping *foot* surrounded by the edge of the body, which forms the *mantle*. In the angle between mantle and foot a row of papillalike *gills* extends into the mantle cavity on each side. An anterior region, which is distinct from the foot and is called the *head*, bears the *mouth*. The *anus* opens posteriorly into the mantle cavity; there are also paired right and left nephridial and reproductive openings. The chiton lives upon rocky bottoms in shallow water, creeping slowly or lying with the edge of the body fixed against the surface upon which it is found. It is well protected from enemies that are unable to tear it from its at-

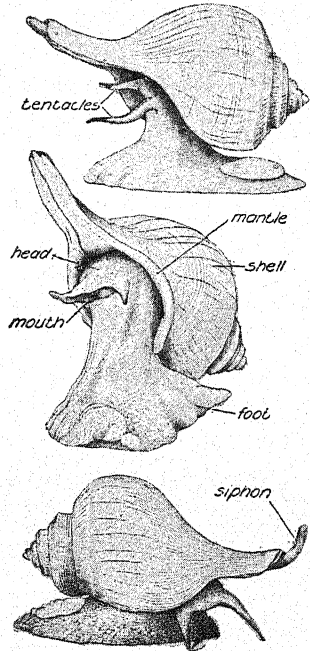


FIG. 318. The marine snail, *Busycon canaliculatum*, in different positions assumed during locomotion.

(Drawn by George T. Kline.)

tachment and devour it whole. The food consists of seaweeds and microscopic organisms, which are eaten with the aid of a tonguelike organ, the *radula*. Internally, the digestive system is a straight tube with paired digestive glands and some lateral outgrowths. The chiton has a dorsal heart and an open circulatory system that is even less developed than that of fresh-water mussels. The single median reproductive organ has paired ducts, and the nephridia are paired. The nervous system consists of a nerve ring and four ventral cords. Another type of amphineuran, represented by the Genus *Neomenia*, includes wormlike animals with a simple organization that is probably degenerate rather than primitive.

The Gastropoda

The commonest representatives of these Mollusca are the many varieties of snails (cf. Fig. 522, p. 718). A snail is covered by a spirally coiled *shell*, from which a bilaterally symmetrical *head* and *foot* protrude during locomotion (Figs. 318 and 319). What thus appears externally is the clue to the general internal organization. The ventral parts of the body are bilaterally symmetrical; the dorsal parts are twisted in a spiral. As a result, the *gills*, the *anus*, and the *nephridial* and *reproductive openings*, all of which must have been located posteriorly in the ancestors of gastropods, have in many cases shifted as much as 180° to lie in the mantle cavity dorsal to the head. The adjustments of the internal anatomy incident to this twisting of a primitively bilateral animal are illustrated by Figure 320.

Among the types of gastropods represented by familiar shells of the ocean are the limpets, such as *Fissurella* and *Patella*, in which the shell is not coiled (Fig. 319 A). This is probably a simplification, because the internal organs are twisted, and because related forms such as the abalone, *Haliotis*, have shells with a simplified spiral. Another type having a twisted body but a shell without much twisting is *Crepidula*, which is called the boat-shell.

The marine gastropods also include a group known as Nudibranchia, which have exposed gills, as their name implies, and in which the shell is absent in the adult (Fig. 321). The gills of nudibranchs are not homologous with those of other Mollusca but are projections from the dorsal surface of the body. The young nudibranch has a spirally coiled shell, which is lost during development, and the dorsal part of the body becomes simplified to a bilateral symmetry. Internally, however, the structure of the adult animal shows a spiral twisting. Nudibranchs are often highly colored and of considerable size, sometimes

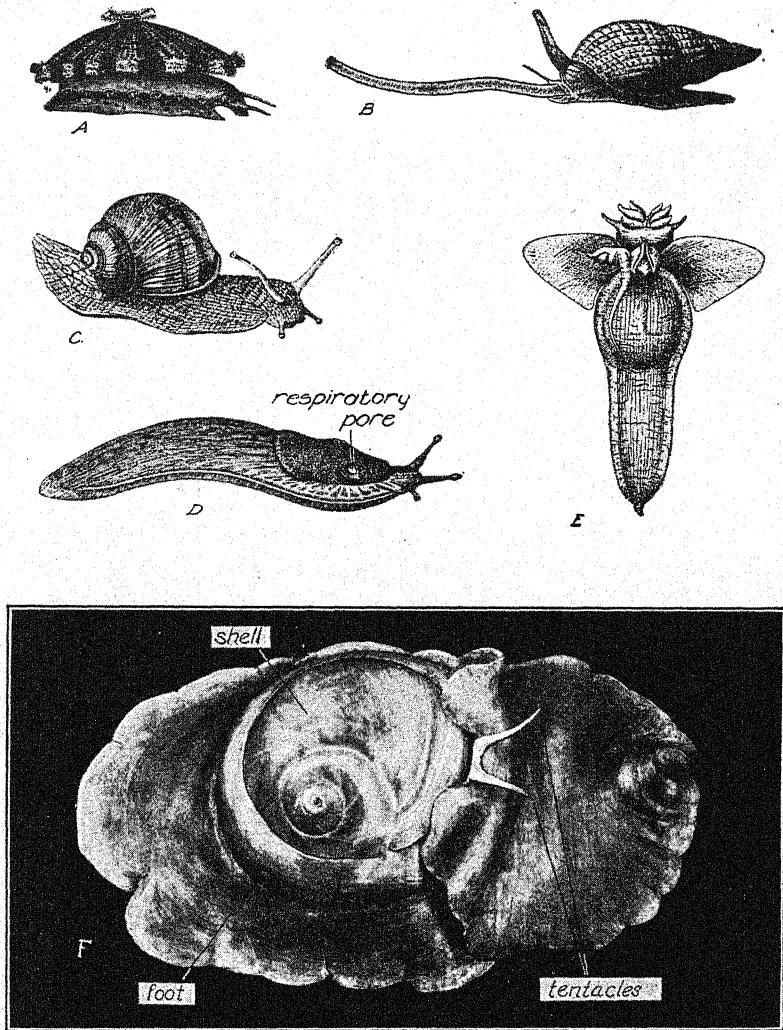


FIG. 319. Representative gastropods. A, *Fissurella maxima*, a limpet. B, *Nassa reticulata*, a marine snail. C, *Helix pomatia*, a common air-breathing land snail. D, *Arion empiricorum*, a slug. E, *Clione limacina*, a marine gastropod in which the shell is absent; ventral view. F, *Polynices (Natica)*, a marine snail.

(A-E, from W. Stempel, "Zoölogie im Grundriss," 1926; F, photograph of model, courtesy of American Museum of Natural History.)

5 or 6 inches in length. Two small subdivisions of the marine gastropods, the Pteropoda and Heteropoda, are pelagic, swimming in the open water by means of a modified foot.

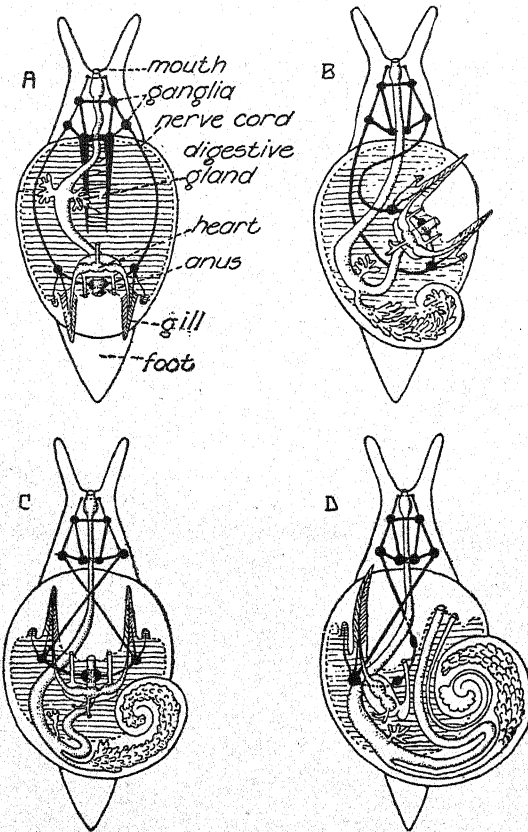


FIG. 320. Spiral twisting of the internal organs of gastropod mollusks through an angle of 180° ; diagrammatic.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

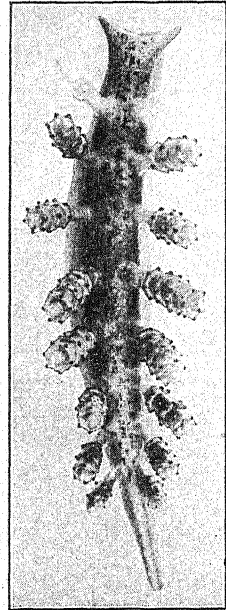


FIG. 321. A nudibranch, *Doto coronata*, as it appears from the dorsal view when fully expanded.

(Photograph of model. Courtesy of American Museum of Natural History.)

In contrast with these marine gastropods, the land snails secure their oxygen not by means of gills but by drawing air into the mantle cavity, which has been modified as a respiratory organ and is sometimes called the "lung." Many fresh-water snails "breathe" in this fashion and are presumably descended from land snails in the manner that such aquatic mammals as the seals are presumed to have descended from land-dwelling ancestors. The land slugs such as *Arion* represent

a modification of this air-breathing type of snail in which the shell persists as a rudiment embedded in the dorsal wall of the body (Fig. 319 D). The asymmetrical opening of the respiratory cavity and the internal structure, together with the spiral shell that is present in the early embryo, make clear the relationship with other gastropods. These land and fresh-water species are called *pulmonate* gastropods because of their manner of respiration, in contrast with the *branchiate* marine and fresh-water gastropods, which possess gills.

The sexes are separate in most gastropods, but some species are hermaphroditic. In many species there seems to be a cycle in which the same animal is now male and now female, as has been noted in a few of the pelecypods (*cf.* p. 421). The eggs, which are laid in capsules or in gelatinous masses, contain an amount of yolk sufficient to provide food for the developing individuals until they become free as miniature snails in the fresh-water species or as free-swimming larvæ, called *veligers*, in some of the marine gastropods.

The Gastropoda illustrate better than any other class the diversity of structure and habitat attained by the Mollusca. Their original home seems to have been the ocean, since the older types are found in that environment and more specialized ones occur in fresh water and upon the land. From this marine environment it appears that some of the descendants penetrated into fresh water and thence to the land, becoming adapted to these new habitats. The pulmonate fresh-water snails are apparently descended from land snails that returned to an aquatic habitat. Other descendants took to free-swimming life in the ocean and gave rise to the existing pteropods and heteropods.

The Scaphopoda

The mollusks belonging to this class were formerly included in the Class Gastropoda. The Genus *Dentalium*, the shells of which have been used as ornaments by many primitive peoples such as the North American Indians, is representative. The animal within its shell might be compared with a limpet (Fig. 319 A) that had become greatly elongated dorso-ventrally and developed a pointed foot (Fig. 322), except that there is no spiral coiling of the internal parts.

The Cephalopoda

The squids, cuttle-fishes, devil-fishes, and nautili, although a small class among the Mollusca, are the most highly developed representatives of the phylum. Some of them, the giant squids, attain a size

unmatched by any invertebrate animals; a recorded specimen had a body 18 feet long and arms as long as 34 feet. One subdivision called the Tetrabranchiata, because members have four gills, is today represented only by the Genus *Nautilus* (Fig. 323). Another, the Dibranchiata, includes all other living cephalopods. In the past there were many tetrabranchs, since upwards of two thousand species, many

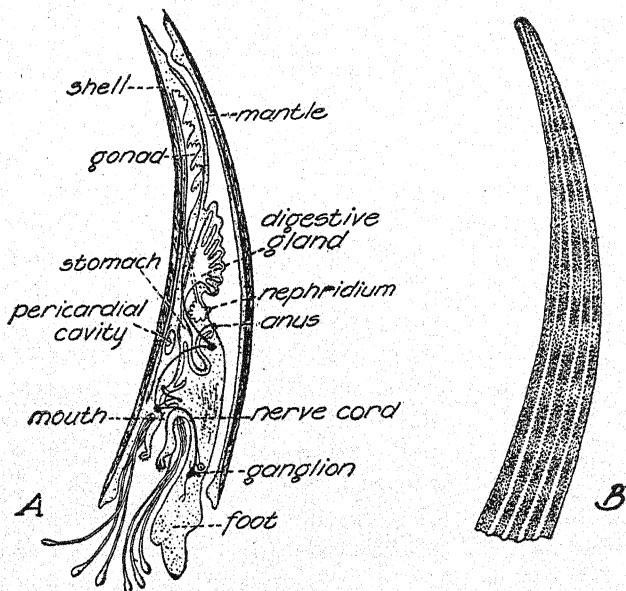


FIG. 322. A, internal structure of the scaphopod, *Dentalium entale*; diagrammatic. B, shell of *Dentalium*.

(A, from W. Stempel, "Zoölogie im Grundriss," 1926; B, redrawn from J. Thiele in W. Kükenthal, "Handbuch der Zoölogie.")

of them highly specialized, are recorded as fossils. Those known as *Ammonites* were one of the conspicuous types of marine life during the Mesozoic Era. The Genus *Nautilus* is not only the lone survivor of this large group; like *Lingula* (p. 405), it is a primitive and long-persisting type.

The squid, *Loligo pealei*, is representative of the dibranchiate cephalopods. At what may be called the anterior end there are ten arms, each with many suckers, surrounding the mouth (Fig. 324). Posteriorly the body tapers, and there is a tail-fin. On the ventral side in the neck region is the siphon. The arms and siphon are modifications of the region homologous with the foot in other mollusks. There are large eyes resembling those of a fish, although they develop in quite a

different manner. The living animal has *chromatophores*, containing brilliant pigments of several colors. These pigment-bearing cells expand and contract, and in this way the color of the entire animal can be altered. The *anus* is located in the mantle cavity near the inner end of the siphon (Fig. 325). A gland called the *ink sac* opens into the intestine near the anus. Apparently, the inky secretion of this gland is discharged from the siphon when the squid is pursued and clouds the water so that the animal may escape the enemy (Fig. 143 F, p. 224). What is called the body of the squid, as distinct from

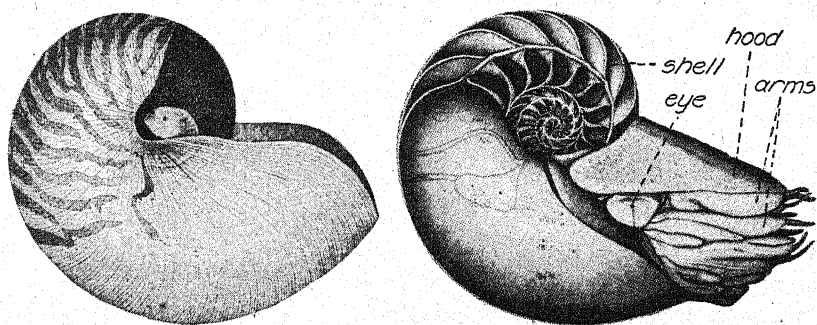


FIG. 323. The pearly nautilus, *Nautilus pompilius*. *Left*, an empty shell, lateral view. *Right*, an animal from which half of the shell has been removed, lateral view.

(From L. E. Griffin, 1898, *Memoirs National Academy of Sciences*, vol. 8.)

its head, is principally the mantle. The parts enclosed by this mantle are really external organs and surfaces of the body as in other Mollusca. Water is admitted into the mantle cavity at the neck region and forcibly ejected through the siphon.

In swimming with the siphon directed forward, the squid can dart backward many feet, propelled by the jet of water that can be extruded through the siphon. When the siphon is directed backward, the animal is propelled forward by the jet. The fin also aids in locomotion, although its more important function seems to be that of a horizontal rudder. A similar, if less effective, rudder is formed by the ten arms, which are held pressed together in a horizontal plane as they extend into the water. Fishes are the common food (Fig. 143 G, p. 224). In feeding, the animal darts forward and seizes the fish, which is then held securely by the arms and their suckers while it is eaten piecemeal.

The internal structure is much specialized. There is a *shell*, called the "pen," which is embedded along the dorsal side and stiffens the

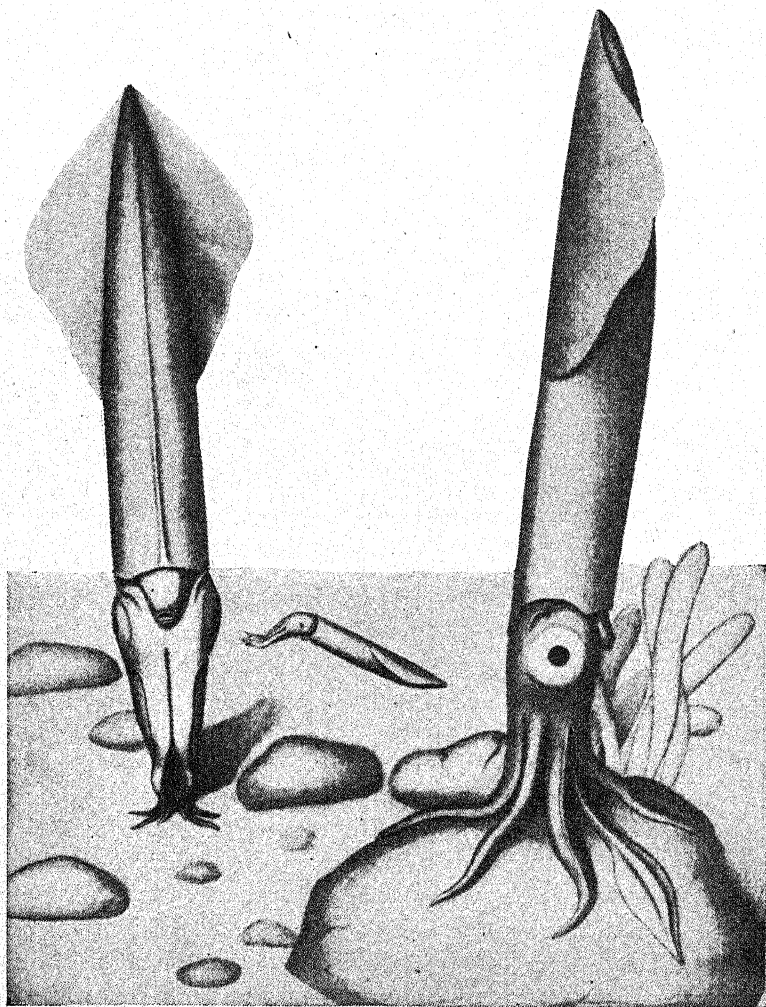
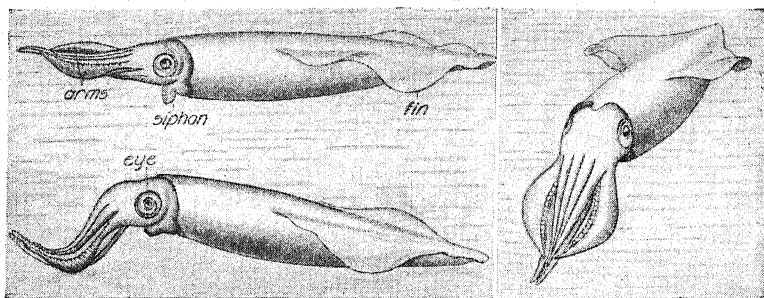


FIG. 324. The squid, *Loligo pealei*. Above, swimming and resting on bottom.
Below, female laying egg-masses, the finger-shaped bodies at right.

(Above, drawn by George T. Kline. Below, from G. A. Drew, 1911, *Journal of Morphology*, vol. 22.)

body. The *digestive system* includes the buccal mass with muscles that move the jaws and the tonguelike radula, the esophagus with the salivary gland, the stomach, the cæcum with digestive glands, and the intestine with its ink sac (Fig. 325). There is an inconspicuous *cælom*, to which the *ovary*, *testis*, and the paired *nephridia* are related. The *circulatory system* is an elaborate closed system. The *nervous system* includes a centralized mass of ganglia in the head region and other ganglia in the body. It is complex but can be homologized with this system in other Mollusca. The greater specialization of the systems related to metabolism and irritability in the squid can be correlated with its active, pelagic existence.

The sexes are separate. Spermatozoa are transferred to the female at the time of sexual union, and fertilization occurs in the oviducts. The eggs are embedded in fingerlike gelatinous masses before laying and are attached on the sea bottom (Fig. 324 Below). As each egg contains a relatively large amount of yolk, the zygote can develop to a miniature adult, which is able to swim and capture food when it becomes free in the water.

Other dibranchiate cephalopods are the giant squids, which inhabit the ocean far from land but are occasionally washed ashore; the cuttlefish, *Sepia*, known for its shells, which are the light calcereous cuttlebones sold as bill-sharpeners for caged birds; the devil-fish, *Octopus* (Fig. 143 E, p. 224), which has eight arms instead of ten as in the squids; and the paper nautilus, *Argonauta* (Fig. 326). The foregoing genera are called Dibranchiata because they have a single pair of gills. Reference has been made to *Nau-*

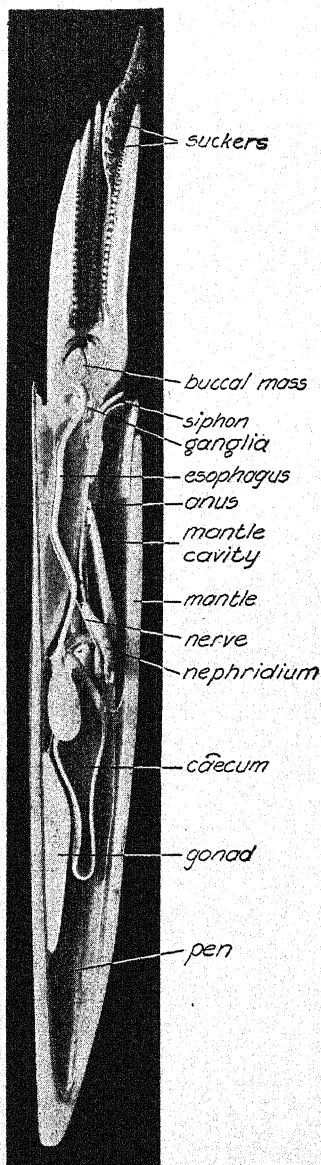


FIG. 325. *Loligo*, cut in half longitudinally.

(Photograph of model. Courtesy of American Museum of Natural History.)

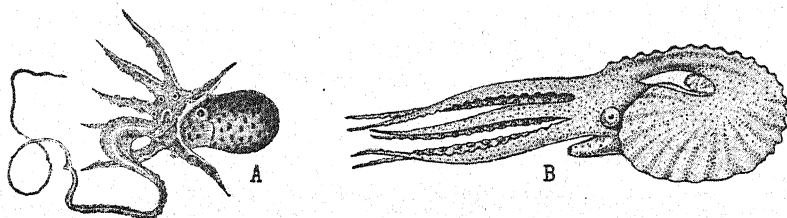


FIG. 326. The cephalopod, *Argonauta argo*. A, male. B, female.

(From W. Stenpell, "Zoölogie im Grundriss," 1926.)

tilus, called the pearly nautilus, as a lone survivor of the Tetrabranchiata, which were once represented by many species (Fig. 323).

The Mollusk Body-plan

A diagram of a mollusk similar to the diagrams illustrating the schematic structure of other animal types would show an animal with a head bearing the mouth and with a body region consisting of a foot and visceral mass covered dorsally by the shell and mantle (*cf.* Fig. 151, p. 235). Within the cavity enclosed by the mantle would be a pair of gills and the paired openings of reproductive organs and nephridia near the anus. There would be at least one digestive gland, a small coelom, a pair of nephridia, an open circulatory system, a nervous system of paired cerebral, pedal, and visceral ganglia with transverse and lateral connections, and a pair of reproductive organs.

Compared with this schematic mollusk, the pelecypod is compressed laterally, with the shell differentiated as two valves, and the head region degenerate. The amphineuran is flattened dorso-ventrally, with reduction of the mantle and division of the shell into transverse plates. The gastropod is more like the schematic type, except for the spiral coiling of its shell and of the dorsal portions of its body. The scaphopod is elongated dorso-ventrally. The cephalopod is elongated dorso-ventrally with the foot specialized as arms and siphon and with other specializations for pelagic life.

CHAPTER 15

THE SEGMENTED WORMS: ANNELIDA

The Phylum *Annelida*, or Annulata, is a group of bilateral, triploblastic, coelomate animals whose most conspicuous feature is the relatively unspecialized metamerism found in many of its species. The coelom is extensive; a pair of nephridia is typically present in each metamere; and the nervous system consists of a pair of dorsal ganglia, circumpharyngeal connectives, and a ventral nerve cord composed of paired ganglia and their connectives, which extends the length of the body. The name annelid, or annulate, is derived from "annulus," a ring, and refers to the ringed appearance in such forms as the earthworms. In all annelids there is some differentiation at each end, but the main part of the body is composed of segments, called the metameres or somites, usually of similar structure internally as well as externally. After being classified for many years in a phylum called the Vermes, or worms, in which were included many other forms to which the name worm was more or less applicable, the annelids are now recognized as a distinct phylum, comprising four classes: the Class *Archannelida*, a small group that is either a primitive or a degenerate type; the Class *Polychæta*, including many common marine species; the Class *Oligochæta*, including the earthworms and the many small annelids of fresh water; and the Class *Hirudinea*, the leeches.

Annelids are typically animals that burrow or crawl upon the bottom in the ocean or in fresh water, although some are free-swimming, at least during the breeding season, and others can live in moist soil. Many species build tubes that serve as permanent habitations; in other species the tube may be forsaken like a burrow and another constructed. Some feed upon prey that is seized with jaws, others upon microscopic organisms that are conveyed to the mouth by ciliated tentacles. In the absence of hard parts other than the chitinous teeth or the tubes constructed by some species, the annelids have left a meager record as fossils, except for their multitudinous tracks upon the mud flats of ancient seas. There are few species in which the size of the individual exceeds that of the largest earthworms, and there are no annelids of great

economic importance unless the earthworms be so regarded because of their effects upon the soil. For the comparative anatomist the annelids are important because of their simple metameric structure. The present chapter describes the clamworm and the earthworm as representative annelids, with particular attention to the earthworm, as exhibiting a structural and functional organization intermediate in complexity between those of the hydra and the frog.

The Polychæta

The name Polychæta, which means "many bristles," is appropriate for annelids of this class, since the more representative polychætes have paired appendages on each somite that are stiffened with many bristle-like structures. The polychætes are almost exclusively marine and are abundant in all the oceans. They are found crawling and burrowing upon the bottom, or living in tubes, or even swimming freely at the surface, according to the species. Worm tracks and burrows preserved in the Cambrian and later rocks indicate that annelids of this type have been abundant since the beginning of the fossil record (cf. Fig. 469, p. 646). Taken as a whole, the polychætes are the most representative of the several classes, since they include generalized types as well as many that are highly specialized.

The Clamworm: *Neanthes (Nereis) virens*. The clamworm represents the Polychæta and also the entire phylum as well as any species that can be selected (Fig. 327). The animal lives just below low-water mark in sand and fine gravel or under stones, without forming permanent burrows. When free in the water, it can swim actively by undulations of its body and movements of the lateral appendages, but it soon burrows again into the bottom, where it lies with only the head exposed. The *mouth* opens ventrally at the anterior end and is encircled by the first somite, the *peristomium* (Fig. 328 A). The dorsal surface of the head region is provided with sense organs in the form of *eyes*, *tentacles*, and *palps*. The *anus* and two *anal cirri*, which are tactile organs like the cirri of the parapodia and the tentacles of the head, are found at the posterior end. The body is composed of *somites*, bearing paddlelike appendages, the *parapodia*, which are the locomotor and respiratory organs (Fig. 328 B). Each parapodium consists of dorsal and ventral parts that are mirror images of each other, although the dorsal part is larger. Toward the anterior end the parapodia are somewhat reduced in size, and toward the posterior end, where the new somites are added as the worm grows, they are not fully developed. There is, however, a pair of parapodia on each somite, except on those

surrounding the mouth and anus. *Nereis* is thus composed of similar structural units repeated throughout the body, but with certain differentiations at each end.

Internally, the *digestive tract* is a straight tube extending from mouth to anus. There is an eversible *buccal region*, a *pharynx* with

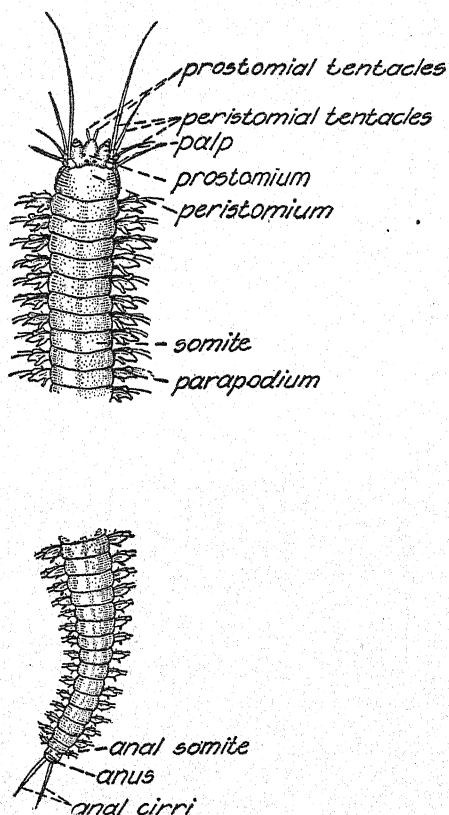


FIG. 327. Anterior and posterior ends of the clamworm, *Neanthes* (*Nereis*) *virens*, from dorsal view.

two *jaws* and numerous small teeth, an *esophagus* into which a pair of glands opens, and from about the twelfth somite posteriorly the tract consists of a simple tube, the *stomach-intestine*. Surrounding this digestive tract is a body cavity that is a well-defined *cœlom* (cf. p. 216) and is divided by *septa* that extend transversely from body wall to gut and by *mesenteries* that extend in the median plane dorsal and ventral to the gut. The septa and mesenteries divide the *cœlom* into a right and a left compartment for each somite of the body. Within these

compartments is a fluid containing amoeboid cells and comparable with the lymph of a vertebrate. The *circulatory system* consists of dorsal and ventral longitudinal blood vessels, with lateral branches to capillaries in the gut and body wall. The blood is thus confined within a closed circulatory system in the same manner as the blood of vertebrates. The circulation within this system is effected by peristaltic contractions of the larger vessels, particularly the dorsal vessel, the pulsations of which can be seen in the living worm to pass from the pos-

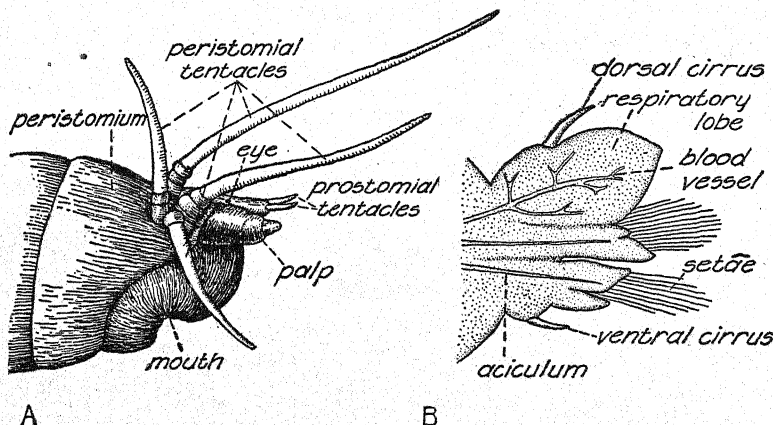


FIG. 328. Head and parapodium of *Neanthes (Nereis) virens*. A, head in lateral view, showing sense organs. B, a single parapodium.

terior to the anterior end. The blood is colored red by hemoglobin in the plasma, not in the blood cells as in vertebrates. The *excretory system* is composed of paired tubes, the *nephridia*, which are found in all the somites except those near the two ends of the body. Each nephridium opens at one end from the coelom and at the other to the outside (cf. Fig. 335). At the inner end is a ciliated funnel, and there are cilia at places within the tube. It is supposed that products of metabolism similar to those eliminated by the kidneys of vertebrates are eliminated from the coelom and so from the body by these organs. The *nervous system* consists of a pair of *ganglia*, the so-called "brain," located dorsally in the head region, *circumpharyngeal connectives*, and a *ventral nerve cord* composed of paired ganglia and their connectives. As the nerves that lead from the ventral cord are similar in every somite, there is a metameric repetition of parts, except in the head region, in the same manner as with the other systems.

The sexes are separate, as they are in most polychaetes. The *ovaries* and *testes* are not permanent structures but are formed at each breeding

season by differentiation from the cells lining the coelom in each segment except at the anterior end of the body. The ova and spermatozoa are discharged into the coelom and pass through the nephridia to the sea water, where fertilization occurs. The zygote develops into a ciliated, swimming larva, the *trochophore*, which settles to the bottom and develops into the young worm (cf. Fig. 343)

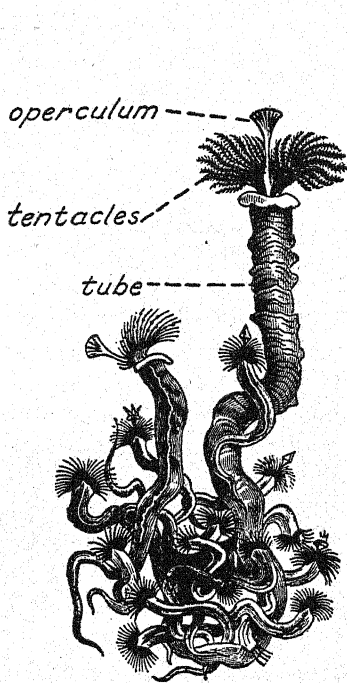


FIG. 329. The tube-building polychæte, *Serpula*, in its tube.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

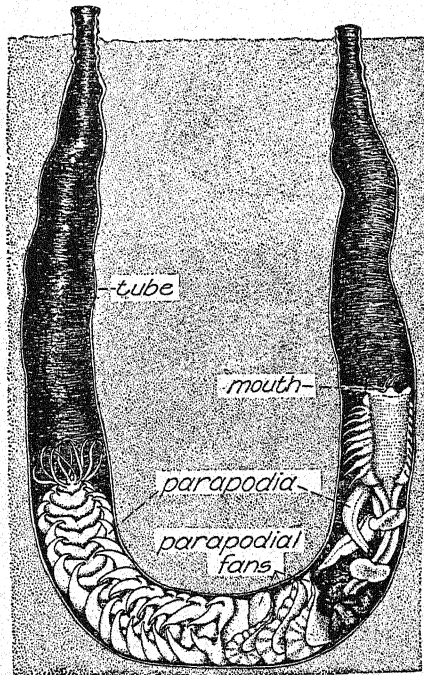


FIG. 330. The polychæte, *Chætopterus*, in its tube.

(Slightly modified from A. S. Pearse, 1913, Biological Bulletin, vol. 24.)

Other Polychæta. In one of the older classifications the polychætes were divided, according to their mode of life and correlated structure, into the Errantia, or errant forms, which are free-living like *Nereis*, and the Sedentaria, which are sedentary and live in tubes or are otherwise fixed in one place. This is still a convenient distinction in a brief consideration of the polychætes, although it is no longer satisfactory as a classification. The worm *Serpula*, which is one example of the sedentary polychætes, lives in a calcareous tube, which may be closed by an operculum when the worm is contracted (Fig. 329). *Ser-*

pula feeds upon microörganisms collected from the water by ciliated tentacles, which also function as respiratory organs. *Cistenides* (*Pectinaria*) lives in a conical tube of cemented sand grains, which is buried in the bottom or dragged about as the worm crawls. In *Chætopterus*, a large worm that forms a U-shaped, parchmentlike tube open at each end and embedded in the sea bottom, three of the parapodia in the midregion are modified as paddles which drive the sea water through the tube in connection with the feeding and respiration (Fig. 330). In these species and in other sedentary polychætes the parapodia and organs of the head are modified in a variety of ways, but the errant polychætes usually have similar parapodia from end to end of the body, as in *Nereis*.

The Oligochæta

The name Oligochæta means "few bristles" and refers to the fact that the bristles are scanty and often inconspicuous. In contrast to the polychætes, which are mostly marine, the oligochætes are found almost exclusively in fresh water and in moist soil. With the exception of the earthworms, most oligochætes are of minute size.

The Earthworm: Habitat and General Activities. Earthworms, such as *Lumbricus terrestris*, are commonly studied as examples of the Oligochæta, because they are large enough for gross dissection and abundant in many localities. They are found in most parts of the world, even on isolated oceanic islands, wherever the ground is sufficiently moist and the temperature not too low. Where they abound, their distribution is determined by the nature of the soil and its moisture. Heavy clay soils and soils in which the underlying rock is near the surface are not favorable. Locomotion is effected by extensions and contractions of the body, aided by the setæ, which can be withdrawn to reduce friction or protruded at an angle to catch against any surface with which the worm may be in contact (*cf.* Fig. 342). As the worm crawls, these movements of the setæ in each region are coördinated with the movements of the body as a whole.

Earthworms burrow in the ground from a few inches to several feet beneath the surface. In winter they are always found below the frost line and are relatively inactive. The burrows usually run straight down for several inches and then wind about irregularly, sometimes reaching a depth of 7 or 8 feet. In loose soil the worm burrows by forcing the pointed anterior end between the particles of earth. In soil of normal consistency the worm excavates the burrow by literally eating its way. The earth which thus passes through the digestive tract is deposited on the surface of the ground as the feces, or castings, which are often seen

where earthworms abound. In this manner lower layers are brought to the surface, and the effect upon the soil resembles that produced by turning with a plough. It is a familiar fact that heavy objects, such as large stones, upon the surface of the ground are found later to be partially embedded, and that a layer of small objects, such as coarse

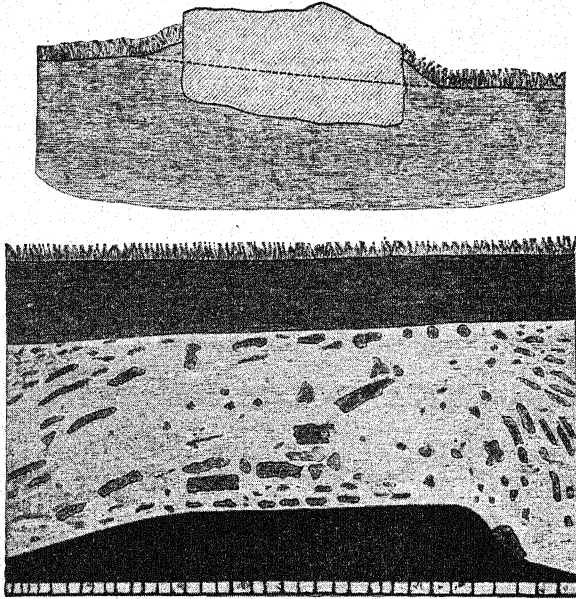


FIG. 331. Burial of objects by earthworms. *Above*, section through a fallen stone of the Druids' "temple" at Stonehenge, England, showing how much it has sunk into the ground (scale: $\frac{1}{2}$ inch equals 1 foot). *Below*, section of part of a Roman ruin at Silchester, England, showing a stone floor upon which was a mass of charred wood, represented in black, and rubbish 27 inches thick, all covered by 9 inches of fine soil.

(From C. Darwin, "The formation of vegetable mould," copyright, 1892, by D. Appleton and Co., reprinted by permission.)

gravel, may be found evenly distributed at a lower level after a period of years. A similar relationship appears in the excavation of ancient ruins (Fig. 331). The gradual sinking of all such objects is apparently due to the bringing of soil from beneath to the surface by earthworms and similar burrowing animals.

Earthworms are nocturnal in their activities above ground, although they sometimes appear in daylight after a shower. During the day they lie in the vertical part of the burrow near the surface, unless engaged in excavating at a greater depth. Often the mouth of the burrow is

plugged with bits of grass or other materials that have been drawn in at the close of the night's activities. With the approach of darkness this plug is pushed aside, and the worm extends the anterior end of its body, exploring the surface in all directions but keeping the posterior end within the burrow. If disturbed, it can withdraw into its burrow by a quick contraction. When the upper levels of the soil are moist and the worms can work at the surface night after night, they secure most of their food in this manner. Leaves, bits of grass, and other vegetable material are smeared with a salivallike fluid and, after being thus softened, are nibbled away by the lips and eaten. Although most of its food consists of vegetation, the earthworm feeds also upon the bodies of insects and other small animals that may be found dead upon the ground; in the laboratory, bits of fresh meat, and even salt pork and bacon are eaten. In times of drought the worms avoid the surface and must depend upon such nutrient material as may be extracted from the soil that passes through the digestive tract as a result of their mining operations.

Under favorable conditions, when the animals are coming to the surface nightly for weeks at a time, the burrow is relatively permanent, and its upper portion may be strengthened by a lining of minute pebbles and other particles, like the walls of an old-fashioned well lined with stones. In times of abundant moisture or when the ground is suddenly flooded, the worms may leave their burrows and are then seen in great numbers on the surface. The popular idea that they "come down in the rain" has thus arisen.

External Structure. The elongated cylindrical body is bluntly pointed at each end and somewhat compressed dorso-ventrally in its posterior region; the *mouth* is at the anterior end, surrounded by the first somite and ventral to a small protuberance, the *prostomium* (Fig. 332). The *anus* is a vertical slit surrounded by the last somite. Dorsal and ventral surfaces may be recognized by the difference in color, the dorsal being darker, and also by a slight flattening that appears throughout the greater portion of the animal in the ventral region (cf. Fig. 342). The body is conspicuously segmented into the metameres, or *somites*, of which there are from 125 to 175 in a full-grown specimen of *Lumbricus terrestris*. A swollen area of glandular epithelium, which is known as the *clitellum* and which secretes the egg-capsules at the time of egg-laying, is usually located between somites 32 to 37. Other glandular areas are found on certain of the anterior segments. The *openings of the ductus deferentes* (vasa deferentia), or male genital ducts, appear on the fifteenth somite as slitlike apertures surrounded by conspicuous lips. The *openings of the oviducts* are much

smaller and are located on the fourteenth somite. Between somites 9 and 10 and 10 and 11 are the *openings of the seminal receptacles*. The

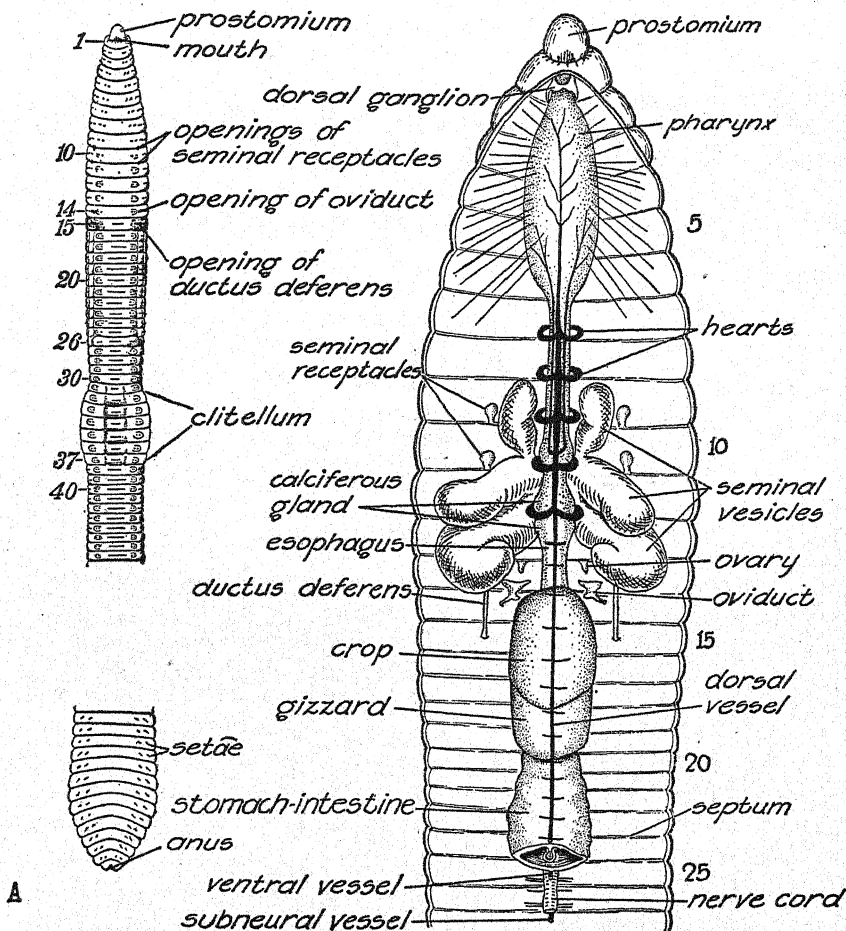


FIG. 332. Structure of the earthworm, *Lumbricus*. Left, anterior and posterior ends, ventral view. Right, internal organs in anterior portion of body, as dissected from dorsal side. The nephridia are not shown (cf. Figs. 335 and 338 B); other vessels of the circulatory system are shown in Figure 334. The numerals indicate the numbers of the somites.

(Left, from W. T. Sedgwick and E. B. Wilson, "General biology," copyright, 1914, by Henry Holt and Co., reprinted by permission; Right, redrawn from same.)

nephridiopores, or openings of nephridia, which occur on each somite except a few at the anterior end, are microscopic and variable in position. There are no structures resembling parapodia, but on each

somite there are four pairs of minute *setæ* comparable with those found in the parapodia of *Nereis* (cf. Figs. 328 and 342). Openings leading from the coelom and called the *dorsal pores* are located on the mid-dorsal line in the constrictions between somites, except in the region of the anterior 10 or 12 somites. The coelomic fluid can thus be exuded and spread over the surface of the body, presumably supplementing the slimy secretion of the epidermal gland cells (cf. Fig. 336 Left).

Structures and Functions Related to Metabolism. Internally, the structure of the earthworm resembles that of *Nereis*, although there are

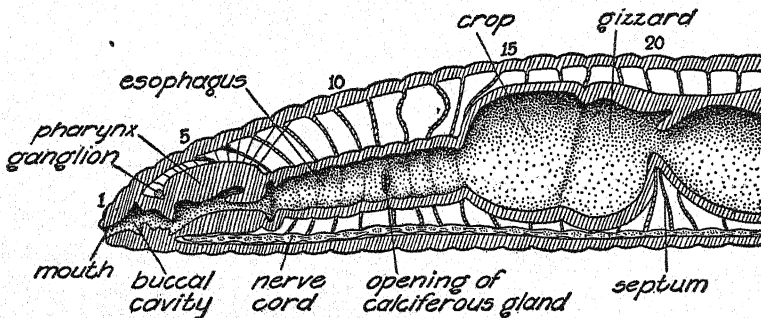


FIG. 333. Anterior end of an earthworm, as if cut in the median plane.

(Redrawn with modifications from A. M. Marshall and C. H. Hurst, "Practical zoölogy," copyright, 1895, by John Murray, printed by permission.)

some important differences. The *digestive tract*, which extends through the body, is differentiated into a *buccal cavity*, a *pharynx*, an *esophagus* with a pair of *calciferous glands* extending through segments 10 to 14 and producing a secretion rich in calcium carbonate, a *crop*, a *gizzard*, and a *stomach-intestine*, which extends posteriorly to the *anus* (Figs. 332 and 333). The buccal cavity and pharynx function in the sucking action by which the animal "nibbles" its food and draws food and other objects toward its burrow by applying the mouth like a vacuum cup. As in other animals, the esophagus is a passageway, the crop a storage place, the gizzard a place where the food particles are reduced in size, and the stomach-intestine the principal region of digestion. *Absorption* occurs by passage of the digested food into the blood vessels of the digestive tract and perhaps directly into the coelomic fluid as well as the blood. The size of the calciferous glands suggests an important function for these organs, although the rôle of their secretion is obscure. It is not clear that any of the functions proposed in later years are more justifiable than Darwin's suggestion that this secretion may serve to neutralize an excess of acid resulting

from the food commonly used by earthworms. The *cœlom* is divided by *septa*, but there are no mesenteries as in *Nereis*. Except in the region occupied by the reproductive organs and anterior parts of the digestive tract, the median ventral portion of each septum is perforated by a large opening, which makes the *cœlom* a continuous cavity.

✓ The *circulatory system* is a closed set of vessels in which the blood flow is maintained by peristaltic contractions of the larger vessels, including certain vessels called "hearts" (Figs. 332 and 334). The *dorsal vessel* rests upon the digestive tract and extends the entire length of the worm. The *hearts* are five pairs of large transverse vessels, located in the seventh to eleventh somites and connecting the dorsal with the *ventral vessel*, which lies beneath the digestive tract and, like the dorsal vessel, extends the length of the animal. Throughout the dorsal vessel the blood flows anteriorly; in the hearts it flows ventrally, but in the ventral vessel it flows anteriorly in the region anterior to the hearts and posteriorly in the region posterior to the hearts. The surprising complexity of the entire system and of the blood flow is apparent from Figure 334. Reference to this figure will show the course of the blood through the nephridia, where at least part of the excretion occurs; and through the body wall where the locomotor musculature is located and where external respiration occurs at the surface of the body, as in the skin of the frog. The red color of the blood is due to hemoglobin in solution, since there are no blood cells in the red blood of the earthworm. The *cœlomic fluid*, which is colorless and lymphlike, contains numerous amœboid cells somewhat resembling the white blood cells of vertebrates (cf. p. 98).

✓ The *excretory system* is like that of *Nereis*, although the nephridial tubules are larger (Fig. 335). Each *nephridium* has a ciliated *nephrostome* at the end which protrudes into the *cœlom* and a *nephridiopore* where the tubule discharges its contents on the outer surface of the worm. Each nephrostome lies in the somite just anterior to the one in which the main part of its nephridium is located, and the tubule passes through the septum before it is folded upon itself in the manner shown in Figure 335. Portions of the tubule are ciliated in addition to the ciliation of the nephrostome, and the outermost section is enlarged like a bladder. The tubule is interlaced with capillaries throughout its length, and the mass of capillaries and tubule is covered with peritoneum. Nephridia are presumed to be excretory organs, but the exact manner in which they function has not been ascertained. An excretory function has been ascribed to the chloragogue cells which cover the stomach-intestine (Fig. 342), but this hypothesis remains to be proved.

Little is known regarding *metabolism* in the earthworm and similar

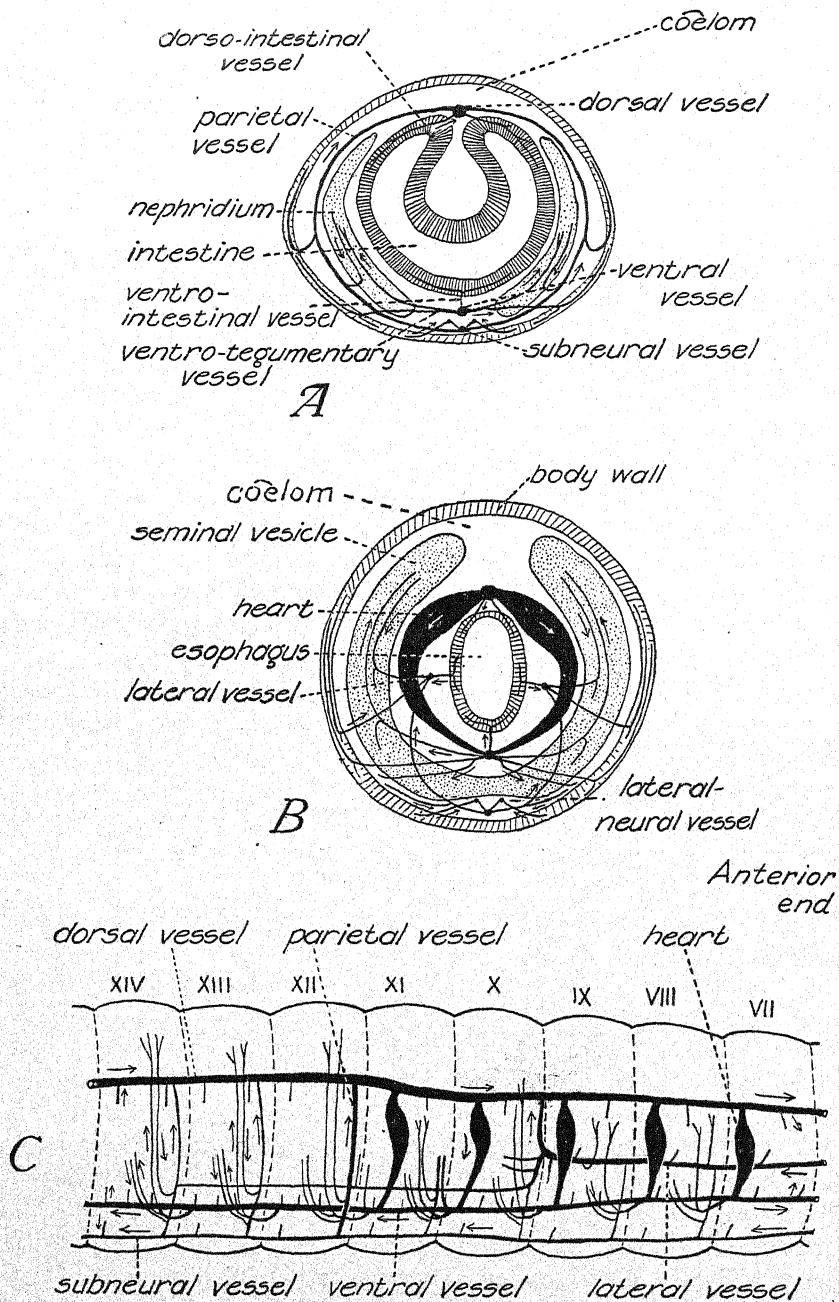


FIG. 334. Circulatory system of the earthworm, *Lumbricus terrestris*. A, cross section in region of the stomach-intestine. B, cross section in region of the hearts. C, lateral view of vessels in somites VII to XIV.

(Redrawn from J. B. Johnston and S. W. Johnson, 1902, *American Naturalist*, vol. 36.)

animals as compared with our knowledge of the metabolic activities in vertebrates. What has been ascertained supports the presumption that the changes by which protoplasm is synthesized and destroyed are

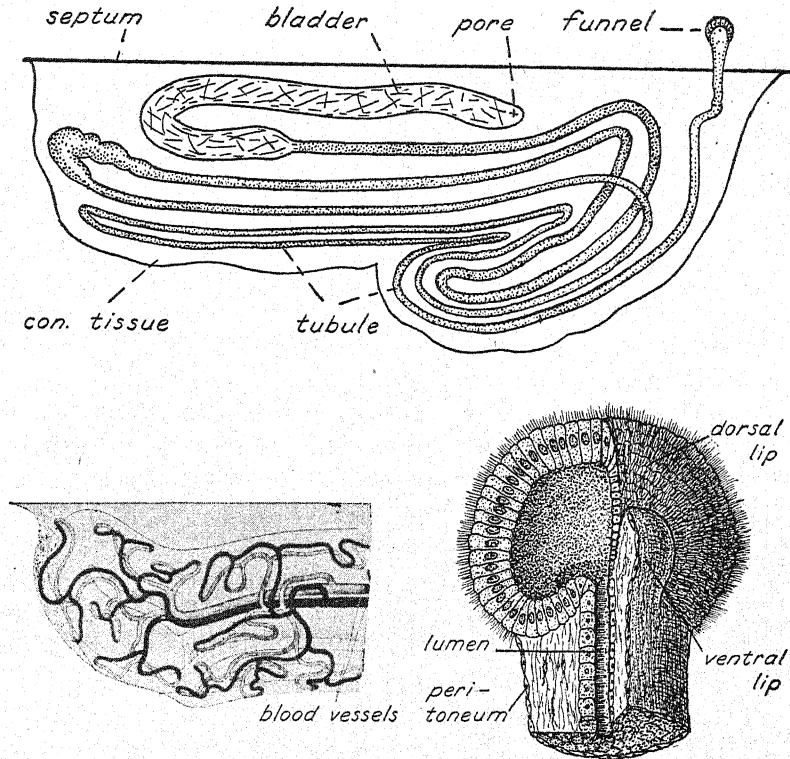


FIG. 335. Nephridium of the earthworm. *Above*, diagram of an entire nephridium, with coils somewhat separated. *Below left*, portion of nephridium showing blood supply; *right*, the nephridial funnel, or nephrostome, by which the nephridium communicates with the coelom; the opening is between the dorsal and ventral lips.

(Redrawn with modifications from G. B. Howes, "Atlas of zoöatomy," copyright, 1902, by Macmillan and Co., Ltd., printed by permission.)

like those occurring in the cells of animals whose functions have been more thoroughly examined. The food that enters the earthworm's digestive tract, as vegetable or animal material and as the organic material of the soil, is *digested* in the digestive cavity by enzymes and *absorbed* through the epithelium lining the cavity into the capillaries of the blood system. Distributed in the blood to all parts of the body, simple foodstuffs pass into the cells, where *assimilation* occurs.

Oxygen, absorbed from the air over the entire surface of the body during *external respiration*, is similarly transported by the blood to all parts where the diffusion into the cells, or *internal respiration*, takes place. *Dissimilation*, or oxidation, occurs within the protoplasm, and the waste products of this disintegration pass into the blood to be carried to the nephridia, the surface of the body, and perhaps to the posterior region of the digestive tract, where *excretion* occurs. In addition to the transfer by the blood vessels of the digested food and of the waste products of dissimilation, a transfer of these substances may be effected by the coelomic fluid. It is not unlikely that digested food passes from the gut cavity into the coelom as well as into the blood capillaries of the digestive tract. Having thus reached the coelomic fluid, the food could be distributed throughout the animal and pass through the peritoneum to the muscle layers of the body wall or into the wall of the anterior part of the digestive tract. In like manner the waste products of dissimilation may pass into the coelom and be excreted by the nephridia. The conspicuous effect of a transformation of energy during dissimilation appears in the movements of the animal. Production of heat can be demonstrated, although it is at a minimum in such an animal as the earthworm. The functioning of different systems in a way to satisfy the metabolic requirements of the protoplasm is fundamentally the same as in the vertebrates.

Structures and Functions Related to Irritability. The *nervous system* with its dorsal ganglia, or "brain," *circumpharyngeal connectives*, *ventral nerve cord*, and *nerves* is essentially like that of *Nereis* (cf. Figs. 332, 337, and 340). The notable difference in the sensory-neural system appears in the head region. *Nereis* is an active, predatory animal. The earthworm is less active and does not capture prey in feeding. In correlation with these different habits, *Nereis* is well equipped with sense organs and has a head region, whereas the earthworm has nothing that can be called a head although the anterior end of its body is the region most sensitive to stimulation.

As may be seen under natural conditions or under controlled conditions in the laboratory, earthworms react to mechanical stimuli, as when they withdraw or extend the body on contact with foreign objects, or when they withdraw into their burrows in response to vibrations transmitted through the ground. Evidence of responses to chemical stimuli appears in their reactions to food, which is to some extent selected as though by a sense of taste, or is even discovered when buried a short distance below the surface of loose soil as though by a sense of smell. Response to light is evidenced by their nocturnal

habits, as well as by withdrawal when a light is flashed upon the surface of the body, particularly the anterior end. Sense organs were long ago recognized upon the surface of the worm's body, although it was not possible to distinguish different types in correspondence with the kinds of stimuli that have been mentioned (Fig. 336). Recently, however, sensory cells that appear to be the ones reacting to light have been discovered, and some progress has been made in separating the sense organs previously known into more than one type.

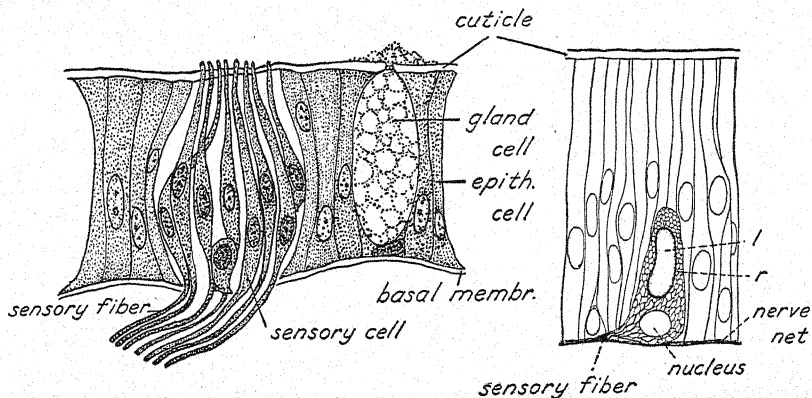


FIG. 336. Sense organs of the earthworm. *Left*, section of the epidermis. *Right*, a light-sensitive cell of the epidermis (cf. Fig. 337), containing a lenslike body (*l*) surrounded by retinalike cytoplasm (*r*).

(*Right*, from W. N. Hess, 1925, *Jour. Morphology and Physiology*, vol. 41.)

The cellular mechanism involved in the foregoing reactions is shown diagrammatically in Figure 337. *Neuro-sensory cells*, the receptors, located in the epidermis receive stimuli and transmit a nerve impulse to nerve cells, the *adjustor neurons* of the ventral cord; these adjustor neurons in turn transmit an impulse to other nerve cells, the *efferent neurons*, which have processes extending to muscle and gland cells, the effectors. Instead, the pathway may omit the adjustor neuron and pass from the neuro-sensory cell directly to an efferent neuron. A comparison with the mechanism in vertebrates (Fig. 39, p. 70) shows that the relationship between cells is essentially the same in the two systems. The neuro-sensory cells of the annelid may be compared with such cells as the olfactory cells of vertebrates (Fig. 46 A, p. 85), which are similarly located in the epidermis and from which nerve fibers extend into the central nervous system. The relationships of the dorsal root cells (afferent neurons) of the vertebrate are more complex, but they likewise transmit impulses into the central system (cf.

Fig. 39, p. 70). The adjustor neurons and the efferent neurons have identical relationships in the worm and the vertebrate. In each, the adjustor neurons are cells with their cell bodies and processes confined to the central system, and the efferent neurons are cells with their cell bodies within the central system but with processes extending outward along the nerves. The cellular mechanism of the nervous system is, therefore, the same in annelids and vertebrates, namely, a *receptor-adjustor-effector system*. The important difference between

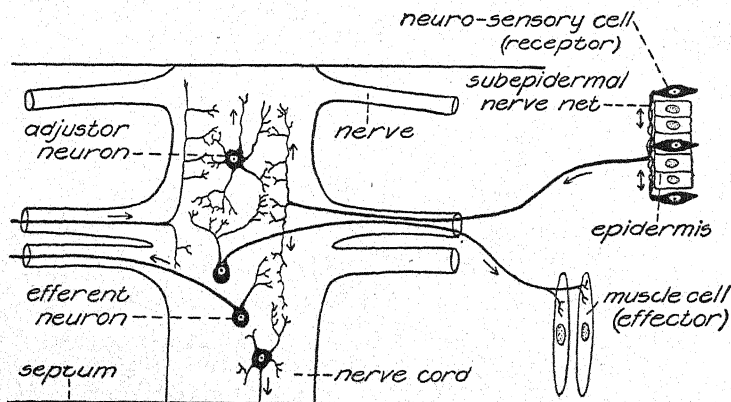


FIG. 337. Sensory-neuro-muscular mechanism of the earthworm; arrows indicate direction of transmission of the nervous impulses.

the two is that the vertebrate has a more elaborate mechanism, notably a much greater number of adjustor neurons.

The Reproductive System, Reproduction, and Development. The earthworm is hermaphroditic (Fig. 338). There are two *ovaries*, attached to the posterior face of the septum near the ventral body wall in segment 13. The *oviducts*, which are located just posterior to the ovaries, are short tubes with funnel-shaped anterior ends which receive the ova as they are detached from the ovary. On the median side of each oviduct is a small sac in which the ova may be held for a time before being "laid" when the egg capsules are formed. Like nephridia, the oviducts pass through a septum and open upon the next segment. There are four *testes* located in segments 10 and 11 and attached to the posterior face of septa in the same manner as the ovaries. In the adult worm, the four testes have become enclosed within a cavity formed by the fusion and overgrowth of three pairs of *seminal vesicles*, which thus partition off a part of the coelom and envelop the testes. In this manner the seminal vesicles provide a

cavity within which the male cells develop into spermatozoa after being detached from the testes in an immature state. The male ducts begin as four large funnels, one posterior to each testis, like the funnels of the oviducts in relation to the ovaries. From each of these

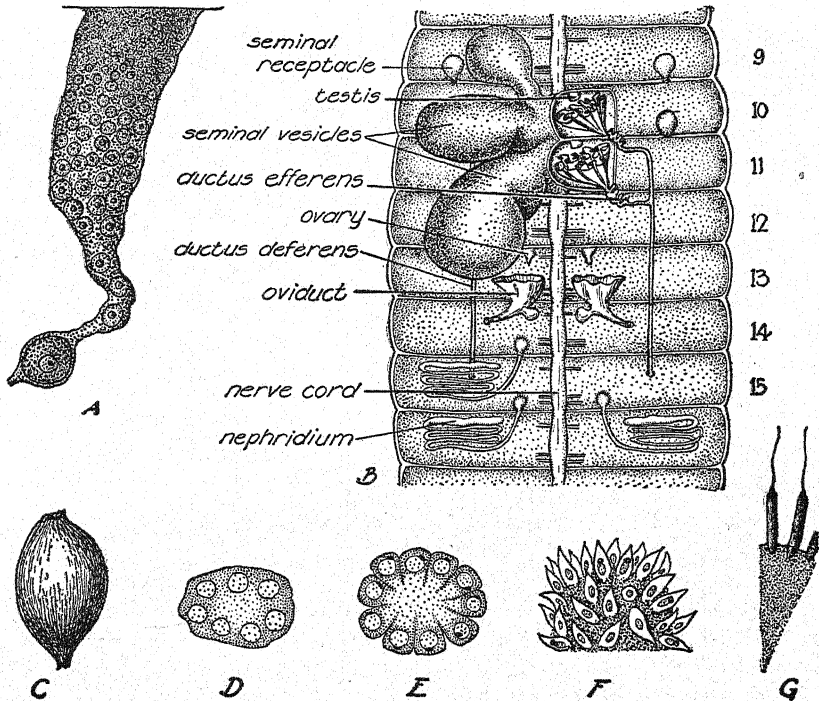


FIG. 338. Reproductive system of the earthworm. *A*, an ovary with oocytes in various stages of growth, the terminal one about ready for detachment from the ovary. *B*, dorsal view of the reproductive system with the cavities of the seminal vesicles of the right side exposed. *C*, an egg-capsule (cf. Fig. 339 C). *D*, multinucleate cell that is detached from the testis and from which spermatozoa differentiate within the seminal vesicles. *E* and *F*, spermatids on the surface of a central mass of cytoplasm remaining from the original multinucleate cell (*D*). *G*, two spermatozoa as they appear attached to the surface of this central mass of cytoplasm.

funnels a *ductus efferens* (vas efferens) leads to the corresponding *ductus deferens* (vas deferens), which opens on segment 15. The final items in this complex system are the four *seminal receptacles*. They are saclike structures which protrude into the coelom in segments 9 and 10 but open only on the outer surface of the worm. Their function is to receive spermatozoa from another individual during sexual

union (Fig. 339) and to retain these spermatozoa until they are used to fertilize the ova of the worm to which the receptacles belong.

During *sexual union* spermatozoa that have accumulated in the seminal vesicles are transferred from each individual of the pair to the seminal receptacles of the mate by way of the seminal grooves (Fig. 339 A). The female portions of the reproductive organs do not

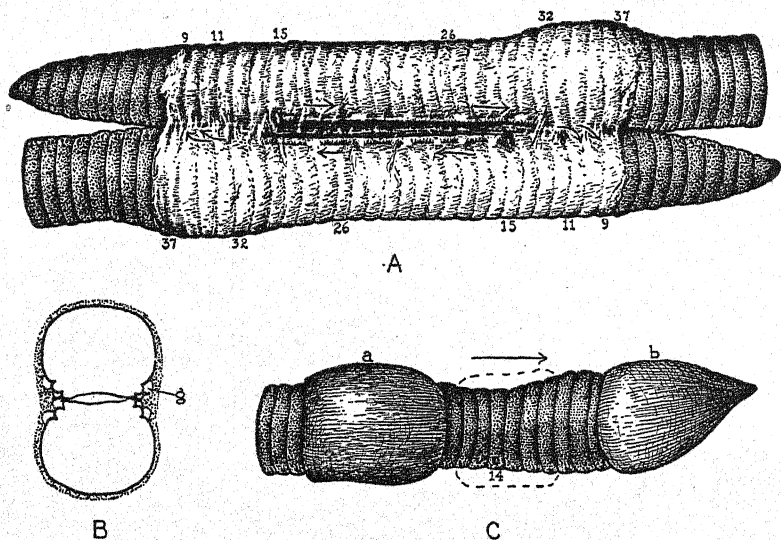


FIG. 339. Sexual union and egg-laying of the earthworm. *A*, two worms encased in mucus secreted by the skin glands, as they appear during exchange of spermatozoa along the seminal grooves as shown by arrows. *B*, transverse section, showing encasing mucus and four seminal grooves (*g*), two on each individual. *C*, formation of egg-capsule and its passage anteriorly (*a* to *b*) until it is slipped off as the fully formed capsule (*cf.* Fig. 338 *C*). Certain of the somites are numbered.

function until later, when the eggs are "laid" and fertilization occurs. At the time of this egg-laying a girdlelike structure is secreted by the clitellum and then pushed anteriorly by movements of the body (Fig. 339 *C*). As this girdle passes the openings of the oviducts on the fourteenth segment, ova are discharged; and, as it passes the openings of the seminal receptacles between the eleventh and the tenth and between the tenth and the ninth segments, the spermatozoa that were received during sexual union are likewise discharged into the space between the girdle and the body of the worm, where fertilization occurs. Finally, the girdle is slipped off the anterior end of the worm and becomes an *egg-capsule* by closure of its two ends. Such a capsule, or "egg,"

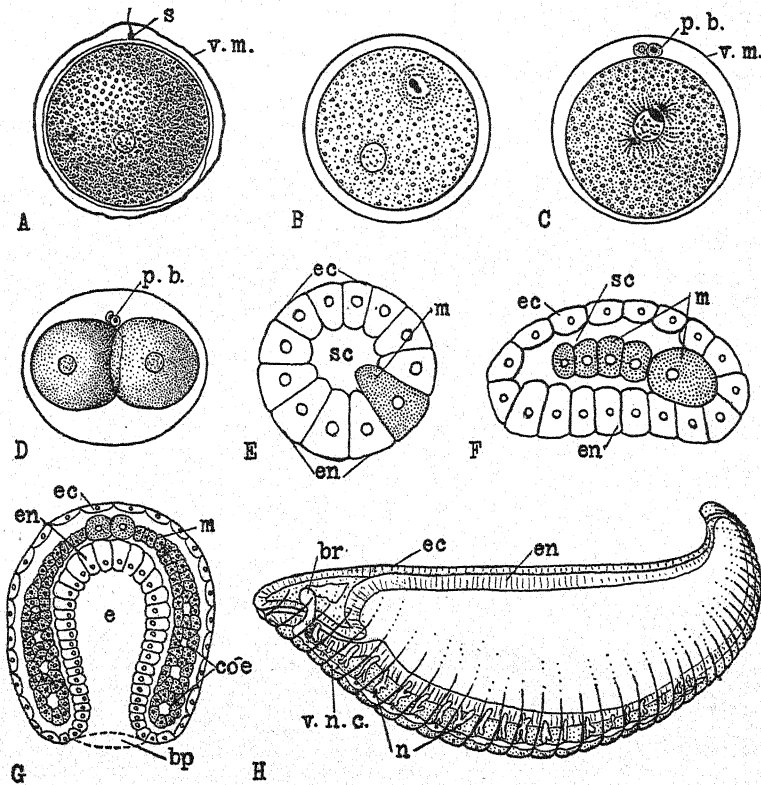


FIG. 340. Development of the earthworm. *A* and *B*, showing entrance of the spermatozoön (*s*) and the fertilization membrane (*v. m.*). *C*, fusion of male and female pronuclei; the polar bodies (*p. b.*) have been formed. *D*, two-cell stage showing polar bodies (*p. b.*) on the surface. *E*, section of an early blastula, showing the cleavage cavity (*sc*) and cells that will give rise to ectoderm (*ec*), endoderm (*en*), and mesoderm (*m*) in later development. *F*, parasagittal section of a late blastula, showing the cleavage cavity (*sc*), the beginning of mesoderm formation (*m*), and cells which will give rise to the ectoderm (*ec*) and endoderm (*en*). *G*, frontal section of an embryo, showing the three primary germ layers, ectoderm (*ec*), endoderm (*en*), and mesoderm (*m*), the gastrocoel (*e*) and blastopore (*bp*), and beginning of the formation of the coelom (*coe*). *H*, late embryo covered with ectoderm (*ec*), showing the mouth, the digestive cavity lined with endoderm (*en*), the dorsal ganglia (*br*) and ventral nerve cord (*v. n. c.*), and the nephridia (*n*).

(Based upon figures and description by E. B. Wilson, 1889, *Jour. of Morphology*, vol. 3.)

contains a nutrient fluid and several zygotes which develop into miniature earthworms before hatching (Fig. 340).

Regeneration. Earthworms can regenerate many somites at the posterior end but only a limited number at the anterior. For example, when pieces are cut from the posterior end of the red-striped earthworm, *Allolobophora* (*Eisenia*) *fætida*, the animal forms a few new somites and then others by additions in the same manner as somites are added posteriorly during growth. When somites are removed at the anterior end, a maximum of only five new ones can be regenerated. A new head may be formed, but the individual never restores the full

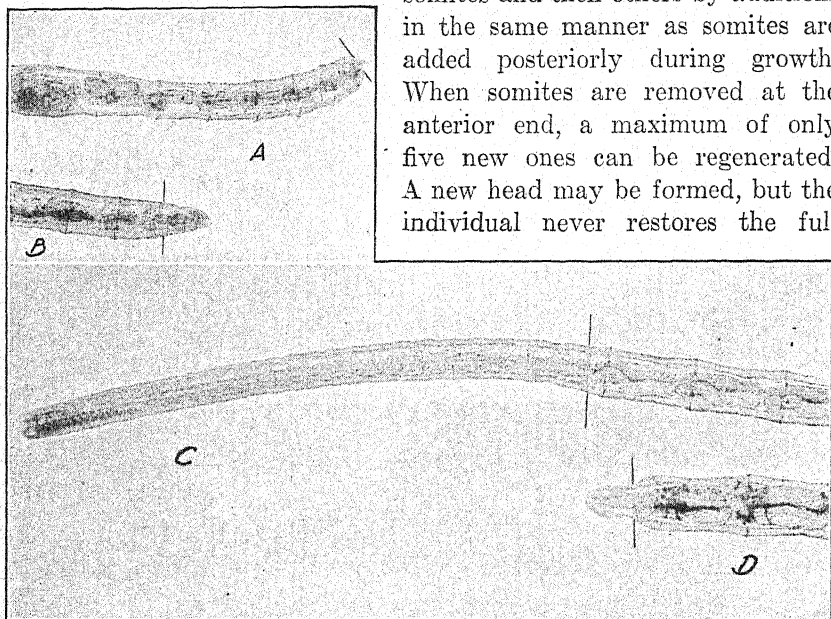


FIG. 341. Regeneration in the fresh-water oligochaete, *Tubifex tubifex*. A, anterior end of an X-rayed worm, showing small knob and absence of regenerated somites after cutting. B, anterior end of a normal worm, showing anterior somites regenerated after cutting. C, posterior end of a normal worm, 21 days after 30-40 somites had been removed; 29 new somites have been formed. D, posterior end of an X-rayed worm, 21 days after removal of 30-40 somites, showing knob formed but no somites. The transverse line marks the place of cutting in each worm.

(A and B, photographs by courtesy of R. G. Stone, *cf.* Jour. of Morphology, 1933, vol. 54; C and D, from R. G. Stone, 1932, Jour. of Morphology, vol. 53.)

number if more than five somites have been removed. When the region containing the reproductive organs is removed, it is not regenerated. In *Tubifex tubifex*, a common fresh-water oligochaete, regeneration in the posterior region is extensive and rapid, an average of thirty-one new somites being formed in thirty-two days (Fig. 341). This regeneration is largely at the expense of the totipotent cells, called *neo-*

blasts, which migrate to the region of the cut and differentiate during the regeneration (cf. p. 354). *Tubifex* can regenerate only three or four somites at its anterior end, and neoblasts do not migrate into such a regenerating area. The importance of the neoblasts in the regeneration of *Tubifex* is confirmed by exposure of the worms to X-rays. When these worms are given a suitable exposure to such radiations, the neo-

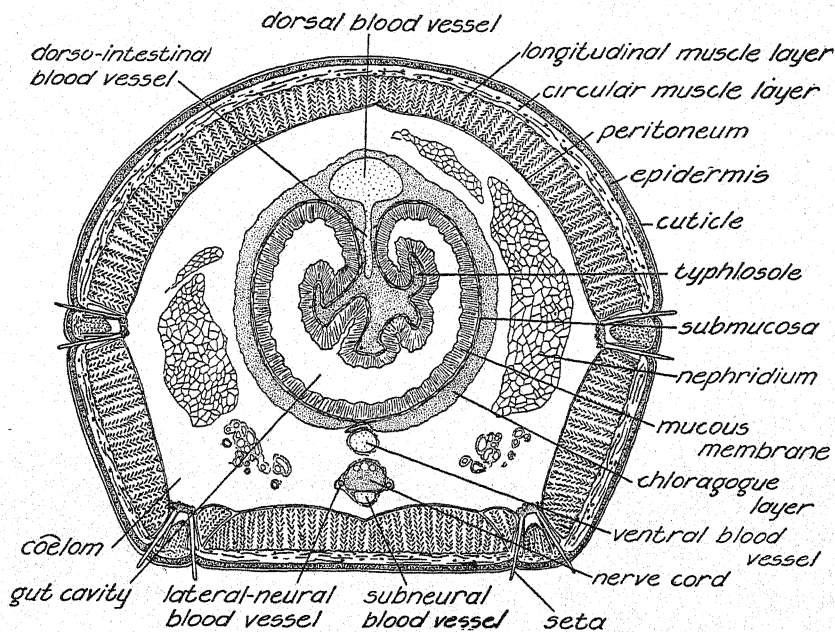


FIG. 342. Cross section of an earthworm in the region of stomach-intestine; diagrammatic.

blasts are destroyed, apparently without injury to other cells, and the individuals thus treated are unable to regenerate (Fig. 341).

Cellular Structure and Functions. The cellular structure of the earthworm includes tissues of the five principal classes—*epithelial*, *sustentative*, *vascular*, *contractile*, and *nervous*—although there is less specialization than in the vertebrates. As shown by a transverse section in the region of the stomach-intestine (Fig. 342), the body wall is covered externally with a delicate, non-cellular *cuticle* which is perforated where gland cells and sensory cells are exposed at their outer ends (Fig. 336). The *epidermis* beneath this cuticle consists of, *columnar epithelial cells*, among which are *sensory cells* and the *gland cells* that secrete the fluid found upon the surface of the worm. Beneath the thin basement membrane, upon which the epidermis rests, is

a *circular muscle layer* composed of *non-striated muscle cells*. Within this muscle layer there is a considerable amount of *fibrous connective tissue* and of *vascular tissue* in the form of *white blood cells* in numerous capillaries. There are no red blood cells, because the redness of the blood is due to hemoglobin dissolved in the plasma instead of being carried in cells. The rich blood supply of this layer is correlated with the external respiration and with the excretion of carbon dioxide through the epidermis. Beneath the circular muscle layer is the *longitudinal muscle layer*, also composed of non-striated muscle cells held together by connective tissue. In transverse section the fibers of this inner muscle layer present a featherlike pattern because of their attachment to sheets of connective tissue, which are seen on edge in such a section. Like the longitudinal and circular muscle processes of a hydra (cf. p. 315), these two muscle layers of the earthworm are responsible for the locomotion and for the many changes in shape and position of the body. The innermost layer of the body wall, the *peritoneum*, is a *squamous epithelium*.

As in the vertebrates, this peritoneum is a continuous layer lining the coelom and covering all the parts that are structurally related to this cavity (cf. Fig. 2, p. 9). The peritoneum thus lines the coelom and covers the coelomic surface of the gut; but in the earthworm and its relatives the visceral portion of the peritoneum is modified to form a columnar epithelium, the so-called *chloragogue cells*, which form the outermost layer of the digestive tract. Beneath these chloragogue cells is a thin *submucosa* made up of connective tissue; non-striated muscle cells, some of which run in a circular and others in a longitudinal direction; and numerous blood capillaries related to the absorption of digested foods. The innermost layer, or *mucous membrane*, which lines the digestive tract, consists of ciliated *columnar epithelial cells* and *gland cells*; this is the layer from which digestive juices are secreted and through which absorption occurs. The digestive and absorptive surface is increased in extent by the presence of a mid-dorsal fold of the gut wall known as the *typhlosole*. It will be recalled that, in the vertebrate stomach and intestine, folds and processes that involve only the mucous membrane and the submucosa similarly increase the surface of the mucosa (cf. Fig. 57, p. 105). In addition to the vascular tissue found in the blood vessels of the earthworm there is the coelomic fluid, which contains *amoeboid cells* and is comparable with the lymph of the vertebrates.

Other Oligochæta. The earthworms are large animals as compared with the great majority of the oligochætes. In contrast with the polychætes the head region of an oligochæte is inconspicuous; there are no

parapodia and few setæ; the individuals of most species are hermaphroditic; and the typical habitat is fresh water. The terrestrial species are found only in moist places; they can be habituated to life in water but not to life upon really dry land. The resemblance of other oligochaetes to the earthworm is such that they need not be considered further.

The Archiannelida

The Archiannelida are small marine annelids which resemble, in their adult stages, the juvenile stages of polychaetes and are supposed

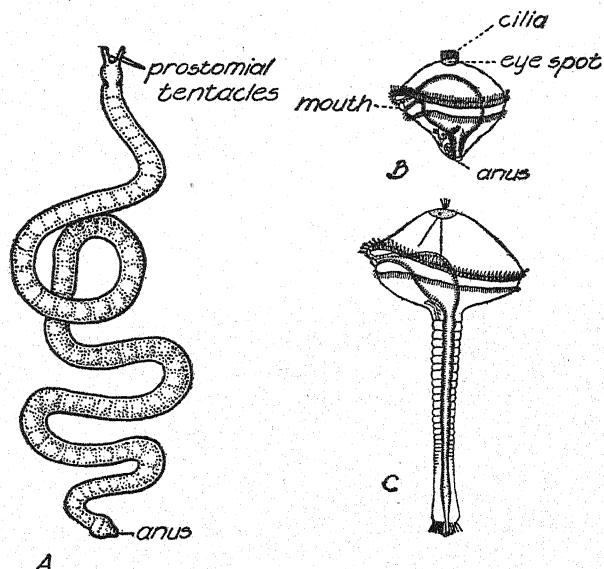


FIG. 343. *Polygordius*, one of the Archiannelida. A, adult worm, from dorsal view. B, trochophore. C, metamorphosing larva.

(B and C from W. Stempel, "Zoölogie im Grundriss," 1926.)

to be a primitive type, although they may have degenerated from a more complex state. *Polygordius*, a representative example, is not distinctly segmented when viewed externally, but internally it shows the metamerism and other features characteristic of annelids (Fig. 343). In the development there is a *trochophore larva*, which undergoes metamorphosis and forms the juvenile worm, as in many of the polychaetes.

The Hirudinea

The Hirudinea, or leeches, are typically fresh-water forms, although a few occur in the ocean and some species have become adapted for life in moist earth. Most of them are temporarily or permanently ectoparasites, although free-living forms are known. The typical annelid structure is modified in correlation with the parasitic habits of the group and otherwise specialized. The body has thirty-three

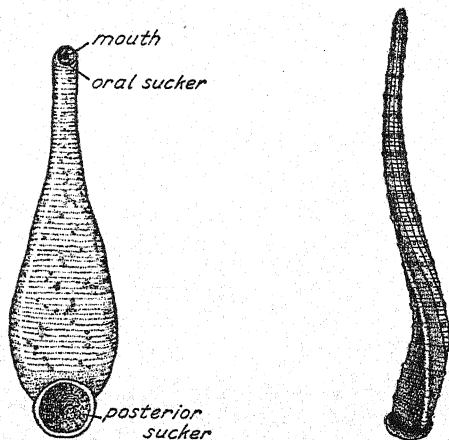


FIG. 344. Representative leeches. *Left*, *Placobdella*, a fresh-water leech; ventral view. *Right*, *Haemadipsa japonica*, a Japanese land leech; shown extended and in one of the positions it assumes when attached by its large sucker and stretching out the body in search of a host.

(*Right*, from W. Stempel, "Zoölogie im Grundriss," 1926. *Left*, from A. C. Chandler, "Introduction to human parasitology," John Wiley & Sons, copyright, 1936, by author, reprinted by permission.)

somites, each divided externally into three or more rings, and is conspicuously flattened dorso-ventrally; there are no parapodia and no setæ. A small sucker surrounding the mouth is used in feeding, and a larger one at the posterior end (Fig. 344 Left) holds the leech securely upon its host or elsewhere. Both of these suckers are used in the locomotion by looping movements, in which the suckers are alternately attached and detached. Or the leech may move by swimming in a characteristic manner. Internally, the nephridia, reproductive organs, and nervous system are clearly of the annelid type, although specialized.

Among the common species, *Hirudo medicinalis*, the "medicinal leech," was so called because it was used for blood-letting when this was a common procedure of physicians. Even today, old people may remember how as children they were fascinated by the leeches kept

alive as office displays by some of the older doctors and used on occasion. Some fresh-water leeches are really dangerous parasites of man and of domestic animals, such as the horse. Entering the mouth with the drinking water, they attach themselves to the mucous membrane of the mouth or pharynx and gorge themselves with blood. It has been estimated that a single leech of one species can hold 8 cubic centimeters of blood. Again, the land leeches found in many tropical countries of the Orient are even more serious pests (Fig. 344 Right). They occur on or near the ground in the dank vegetation of the rain forests and fasten themselves to men and animals that pass by.

The Annelid Body-plan

The type of structure that is found in annelids is important for comparison with the simpler type that occurs in turbellarians and with the more complex type found in vertebrates. In comparison with a turbellarian the annelid is metameric, and its mesodermal region is differentiated into outer and inner layers, between which is a body cavity known as the coelom (*cf.* pp. 216 and 345). In comparison with a vertebrate the annelid shows a similar relationship of ectodermal, mesodermal, and endodermal regions. An annelid such as *Nereis* consists of somites, most of them alike in every detail. The only divergence appears at the two ends of the animal as the characteristic antero-posterior differentiation. The coelom is a cavity, lined with peritoneum and connected to the outside by the nephridia, which also function as reproductive ducts. The germ cells arise from the wall of the coelom. The metamerism shows greater specialization in some species, as may be seen when parts such as the reproductive organs are located in a limited region of the body. The coelom may appear as a continuous cavity through loss of the septa or may be almost obliterated by growth of mesodermal tissue, but conditions like these appear to have arisen by evolution from the more generalized type. In a vertebrate, on the other hand, metamerism is evident only in such parts as the nervous, muscular, and skeletal systems, and the coelom is variously modified by separation into compartments and by loss of its primitive relationships with the reproductive and excretory ducts. In the Arthropoda we shall find that the metamerism is little specialized in some members of the phylum and much specialized in others, and the coelom is so much reduced that its nature in the ancestors of arthropods is problematical. The Annelida present the most generalized type of metamerism and of coelom to be found in any of the phyla in which these anatomical features are represented.

CHAPTER 16

THE ARTHROPODA

The Arthropoda are bilateral, triploblastic, metameric animals, like the Annelida, but with a coelom that is reduced and modified and with an exoskeleton that is molted periodically. The name Arthropoda, which means "joint-footed," refers to another conspicuous feature, the jointed appendages. Disregarding the more elaborate classifications that seem necessary to specialists, we may divide the phylum into the Subphyla *Branchiata*, *Tracheata*, and *Arachnida*. The Subphylum Branchiata includes the single Class *Crustacea*, of which the crayfish, lobsters, crabs, and a host of smaller forms are representative. The Subphylum Tracheata includes the Class *Onychophora*, which are primitive wormlike forms; the Class *Myriapoda*, or "hundred-legged worms"; and the Class *Insecta*, or locusts, beetles, butterflies, and the innumerable other forms of insect life. The Subphylum Arachnida includes only a single class, called the Class *Arachnida*, which consists of such forms as the horseshoe crabs, spiders, ticks, and mites.

The habitat of arthropods is more diversified than that of any other phylum, except the Chordata, since representatives are found abundantly in the ocean, in fresh water, and on land, while most of the insects are adapted for flight. In correlation with this diversified habitat the species present great variety of habits and structure, although the arthropod type of organization is well defined by the metamerism, the skeleton, and the appendages. No other phylum of the Animal Kingdom approaches the arthropods in the number of species included. It has been estimated that the number of species of insects alone is over 1,000,000, as compared with a total of some 35,700 species of the Chordata and 60,000 of the Mollusca. If to the insects be added the 16,000 species of crustaceans, 16,000 species of arachnids, and 2000 species of myriapods, the total is much larger than that of all other species of animals. We are accustomed to think of the vertebrates as the dominant forms of terrestrial life at the present day. They are far exceeded in numbers of species and individuals by the insects, which so swarm upon the land surface as literally to contend with the vertebrates for possession of the earth. The arthro-

Pods are of considerable economic importance. Crustacea, such as lobsters, crabs, and shrimps, are a source of food. Certain insects produce silk, others produce honey, and through the agency of insects many plants useful to man are pollinated. On the other hand, the phylum contains species that destroy almost every form of vegetation, others that are parasitic on man and his domestic animals, and still others that transmit diseases to man.

The first arthropods, as yet known from the fossil record, were the familiar trilobites (Fig. 471 B, p. 650), which were abundant in Cambrian and Silurian times (*cf.* Fig. 469, p. 646) but later became extinct. Since the trilobites were evidently complex and highly specialized forms, it is presumed that they were preceded by simpler forms and hence that representatives of this phylum existed at a much earlier period. The fossil record of arthropods from the Cambrian Era to the present is limited, presumably because most arthropods have not had skeletons that were likely to be preserved. Nevertheless, there is a considerable record of these animals. A unique example is the preservation of insects embedded in amber and perfect in every external feature.

The Crustacea

Taken as a whole, the members of this class represent the simplest type of arthropod, although many species of crustaceans are highly specialized. The Crustacea are, for the most part, aquatic animals and include the principal marine representatives of the phylum. During their evolution they seem to have spread from the ocean, as their primitive habitat, to fresh water and thence in a few instances to the land in the same manner as the gastropods among Mollusca. The two principal types of Crustacea, known as *Entomostraca* and *Malacostraca* in some of the older classifications, will be considered after we have examined the crayfish as a representative species.

The Crayfish: Habitat and Activities. A reference to crayfishes appears in the writings of Aristotle, who mentioned the "small lobsters that breed in the rivers." Although these forms are called crayfishes or crawfishes, they might be called lobsters, so close is the resemblance, particularly to the American lobster, *Homarus americanus* (Fig. 345). Crayfishes abound in streams and fresh-water ponds upon all the continents and many of the larger islands, such as Tasmania, New Zealand, and Madagascar, although they are dependent upon a sufficient amount of calcium carbonate in the water and other environmental conditions. Species of the Genus *Cambarus* are widely distributed in the more temperate regions of North America east of the

Rocky Mountains, and species of the Genus *Potamobius* (*Astacus*) are found in the streams of the Pacific slope. The account that follows is applicable to the common species of *Cambarus*.

In nature the crayfish is found crawling upon the bottom or concealed under stones and in the burrows which it excavates in the banks of ponds and streams. Some species, such as *C. gracilis*, burrow for many feet into the bank, constructing air holes that appear as chimney-like masses of mud brought up and deposited around the opening.

In moving about upon the bottom, the crayfish walks slowly forward with its great claws held in front of the body and darts backward through the water by sudden strokes of the tail-fin. One such stroke will carry the animal many feet and so out of danger. As the crayfish thus shoots through the water, the folded abdomen offers little resistance; and, when it comes to rest upon the bottom, the abdomen expands, ready for another stroke. Crayfishes respond quickly to visual stimuli; but the antennæ, which are tactile organs, the antennules, which contain the statocysts or organs of equilibrium, and the chemoreceptors must be more important sense organs than the eyes in the crevices and burrows, where little light penetrates. In feeding, the crayfish captures animals, such as aquatic insects and fishes, by lying in wait and seizing them with its claws, or it may feed upon animals found dead upon the bottom. It may also feed upon water plants.

Although the crayfish is primarily an aquatic animal, it thrives best in the laboratory if kept where it can crawl in and out of the water and will often remain exposed to a moist atmosphere for hours. Along a stream at night, crayfishes are sometimes seen upon the bank near the water, and they occasionally make nocturnal expeditions of some length upon land, probably in search of food. In spite of their defensive claws and their mode of escape by darting backward, crayfishes are captured by many animals. Toads, frogs, salamanders, turtles, and water-snakes prey upon them, as well as fishes. Even birds, such as some of the herons, have been observed to capture crayfishes, and the omnivorous raccoon devours them. Man, however, is their most serious enemy, because he uses them as food or destroys their normal habitats by drainage and similar projects. But wherever the conditions are fairly normal, crayfishes usually thrive even in the face of attempts at extermination. In Europe they have long been esteemed as food and are likely to be eaten in greater numbers in the United States if the lobster and shrimp fisheries decline. Like other animals, they are often infested with parasites, notably oligochaete worms of the Genera *Branchiobdella* and *Bdellodrilus*, and certain nematodes.

General Structure. Externally, the animal consists of an anterior *cephalothorax* and a posterior *abdomen*. The cephalothorax is divisible into a *head* and a *thorax*. These three regions of the body are composed of *metameres*, or *somites*, each bearing a pair of jointed appendages, although the metamerism is apparent only in the abdominal

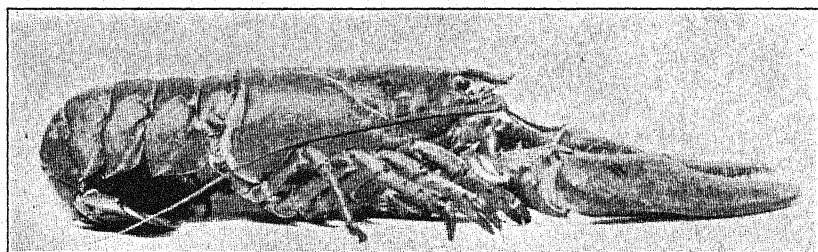
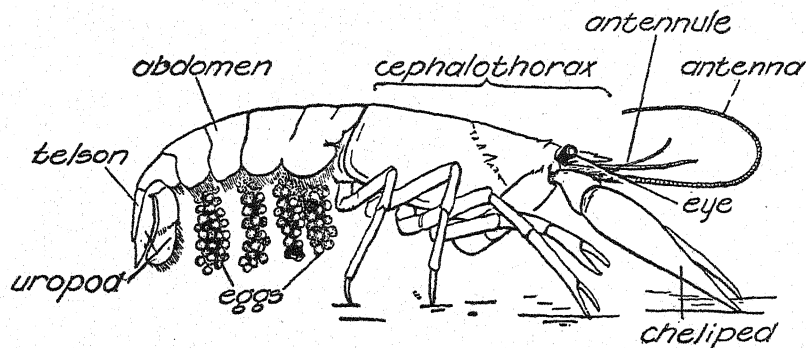


FIG. 345. Crayfish and lobster. *Above*, a female crayfish in attitude assumed during aëration of the eggs, which are attached to the swimmerets. *Below*, an adult female American lobster, in position assumed when at rest upon bottom of an aquarium; on a scale much less than that of the crayfish.

(*Above*, from E. A. Andrews, 1904, *American Naturalist*, vol. 38. *Below*, from F. H. Herrick, 1895, *Bulletin U. S. Bureau Fisheries*.)

region (Fig. 345). In the cephalic and thoracic regions the somites are fused dorsally, and the skeleton appears as the *carapace*, which covers the dorsal and lateral surfaces of the cephalothorax. The boundary between the head and thorax is marked by a groove upon the carapace. Anteriorly, the carapace terminates in a pointed region called the *rostrum*. The paired *eyes* and two pairs of sensory appendages, the *antennules* and *antennæ*, project laterally and anteriorly from their attachments ventral to the rostrum. The appendages about the mouth, which are modified to assist in food-getting, are known as the oral appendages. Of these the *mandibles* and the first and second

maxillæ are located on the head; the first, second, and third *maxillipeds* are located on the anterior part of the thorax. The maxillipeds are followed by the great claws, or *chelipeds*, which are the first of the five pairs of walking legs, or *pereiopods*. The abdomen bears five pairs of

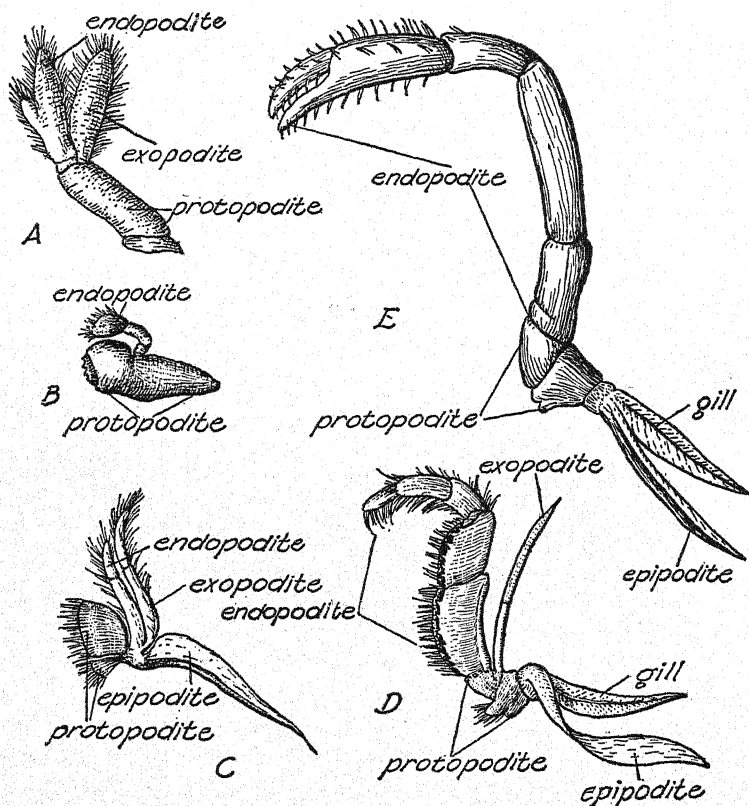


FIG. 346. Appendages of the American lobster, *Homarus americanus*. A, second swimmeret. B, mandible. C, first maxilliped. D, third maxilliped. E, second pereiopod.

delicate appendages, the *swimmerets*, to which the eggs are attached in the female during the breeding season. In the male the two anterior pairs of abdominal appendages are modified as copulatory organs. The large paddlelike appendages upon the most posterior somite are called the *uropods*. The body terminates posteriorly in a median portion, the *telson*, which is without appendages and bears the *anus* upon its ventral surface. The uropods and telson together constitute the powerful tail-fin by means of which the animal darts backward through the water.

Of these nineteen pairs of appendages, five belong to the head, eight to the thorax, and six to the abdomen. There are thus nineteen somites indicated by the appendages, and this count is confirmed by the nineteen pairs of ganglia that appear during the development, although some are not distinguishable in the adult animal. When the structure of the appendages is compared, it is found that all have a similar plan (Fig. 346), although some are so greatly modified that the homologies are not clearly recognizable until one examines the stages of develop-

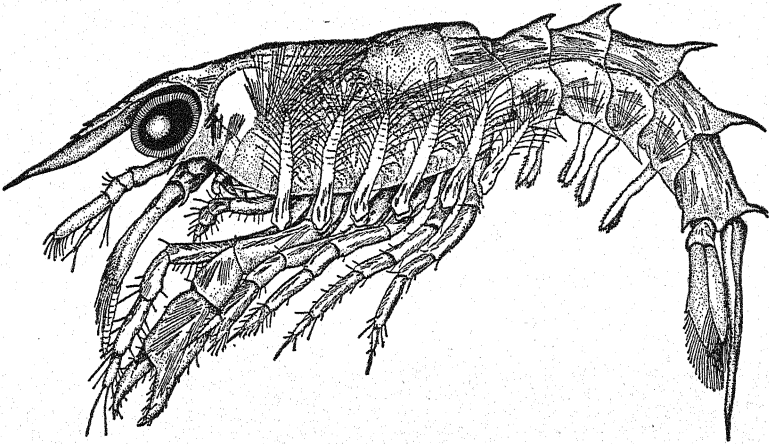


FIG. 347. Young American lobster, *Homarus americanus*, at a stage when exopodites are present on the pereopods.

(From F. H. Herrick, 1895, Bulletin U. S. Bureau Fisheries.)

ment. The simplest of all the appendages are the swimmerets, which show the fundamental plan of a basal *protopodite* consisting of two segments and bearing an *exopodite* and an *endopodite*. In the pereopods, the protopodite is divided into two segments and the endopodite into five; the exopodite is missing in the adult, although present until a late stage of development (Fig. 347). In the maxillipeds the three fundamental divisions, protopodite, exopodite, and endopodite, again appear. In the maxillæ and mandibles, it is again necessary to refer to the development if one wishes to be sure of the homologies. The mandible, for example, consists of protopodite and endopodite in the adult, but an exopodite is present during development. The antennæ show the three fundamental parts, with the endopodite greatly elongated. The antennules are similarly divided into a basal segment bearing two terminal portions, but their homology with appendages is uncertain, because the antennules may have originated as sensory

appendages of the head and not as lateral outgrowths of the somites like all the other appendages. The antennules would then be classed with the eyes, as originally sense organs and not appendages.

Removal of the carapace exposes the *gills* as a series of lateral outgrowths on the thorax (Fig. 349). These gills are really external organs, covered by an overgrowing portion of the body, the carapace, which encloses them in a gill cavity in the same manner as the mantle encloses the gills of a pelecypod (*cf.* Fig. 299, p. 417). In the crayfish there are three kinds of gills: *podobranchiæ*, arising from the epipodites, which are outgrowths from the basal segments of the thoracic appendages; *arthrobranchiæ*, arising from the joints where the thoracic appendages are attached to the body; and *pleurobranchiæ*, arising from the sides of the thorax (Figs. 346 and 349). Typically, each thoracic segment bears one pair of *podobranchiæ*, two pairs of *arthrobranchiæ*, and one pair of *pleurobranchiæ*; but modifications of this plan are frequent, especially loss of the *pleurobranchiæ*.

In concluding this account of the external features, it should be emphasized that the skeleton is a continuous structure that covers the entire external surface of the animal and is continued for some distance into the digestive tract from the mouth and anus. Even the most delicate external parts, such as the gills, are covered by a thin layer of the skeleton. Between the somites of the abdomen and between the segments of the appendages, the skeleton is thin and flexible and composed of chitin, which is the distinctive substance in the skeletons of arthropods. In its thicker portions the skeleton of a crustacean such as the crayfish is hardened by addition of calcium carbonate. This exoskeleton of the arthropod, like the cuticle of an annelid, is non-cellular and is secreted by the cells of the epidermis (*cf.* Fig. 342, p. 461). The exoskeleton of the crayfish may increase in thickness, but it cannot stretch laterally except in the early stages of its formation before the calcium carbonate has been deposited. As a result of this mechanical relationship of body to skeleton, growth cannot occur by continual additions to the skeleton as it can with the exoskeleton of a mollusk or the endoskeleton of an echinoderm. Hence the crayfish, like other arthropods, periodically secretes a new skeleton beneath the old one, which it molts, including the linings at each end of the digestive tract. In the few hours after such a molt is completed the crayfish becomes a size larger, and, as the skeleton hardens during the days that follow, the animal assumes again its familiar condition. During its soft-shelled state the crayfish is defenseless and usually remains in its burrow or otherwise concealed. The soft-shelled crabs, which are so

esteemed as food, are merely crabs captured soon after molting and before the hardening of the shell.

Structures and Functions Related to Metabolism. The *digestive system* consists of the digestive tract and appended glands (Fig. 348). A short *esophagus* leads from the mouth to the *stomach*, the anterior portion of which contains the *gastric mill*. This structure has teeth, formed by thickenings of its skeletal lining, and functions in the final mastication of the food. Large *digestive glands* open into the anterior region of the *intestine*, which extends as a straight tube to the *anus*

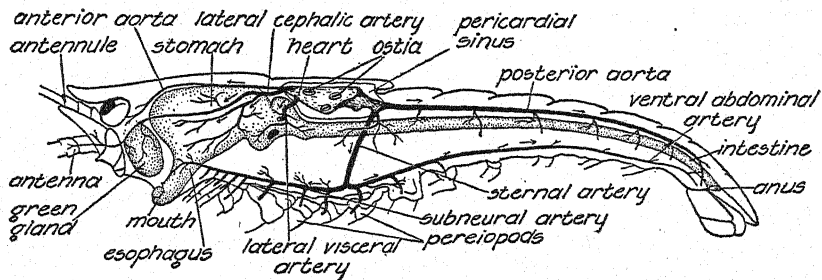


FIG. 348. Digestive and arterial systems of the crayfish; arrows indicate the direction of blood flow (cf. Fig. 349).

(Redrawn with modifications from G. B. Howes, "Atlas of zootomy," copyright, 1902, by Macmillan and Co., Ltd., printed by permission.)

(cf. Fig. 349). The portion of the intestine into which the digestive glands open is the only region of the tract not lined by the exoskeleton, and the mucosa of this region is the only mucosa that arises from the endoderm during development. Between the muscles and other internal organs extensive cavities are found through which the blood flows in its return from the outer ends of the arteries to the heart. These cavities are called *hemocœls* because they contain blood. What seems comparable with the *cœlom* of annelids (cf. p. 216) is found as the rudimentary sacs at the inner ends of the excretory organs and perhaps as the cavities within the ovaries and testes. *Digestion* occurs in the gastric mill and within the larger cavities of the digestive glands. *Absorption* seems to take place from these organs into the hemocœles, from which the blood flows eventually into the heart and arteries.

The *circulatory system* consists of definite vessels in some regions, whereas in other regions the blood flows in the spaces between cells and in the hemocœls. The *heart*, the wall of which is perforated by three pairs of openings, or *ostia*, lies dorsal to the intestine in the thoracic region and is surrounded by the *pericardial sinus* (Fig. 348). From the heart, blood is carried anteriorly by the median *anterior aorta* (ophthal-

mic artery) to the head, by the paired *lateral cephalic arteries* (antennary arteries) to the stomach, green glands, and anterior muscles, and by the paired *lateral visceral arteries* (hepatic arteries) to the gonads, the anterior part of the intestine, and the digestive glands. Blood is carried posteriorly from the heart in the median *posterior aorta* (dorsal abdominal artery), which gives off branches to the muscles, intestine, and all the abdominal appendages except the most anterior pair. From the posterior part of the heart a single *sternal artery* (descendent artery) passes ventrally and gives rise to the *subneural artery*, which

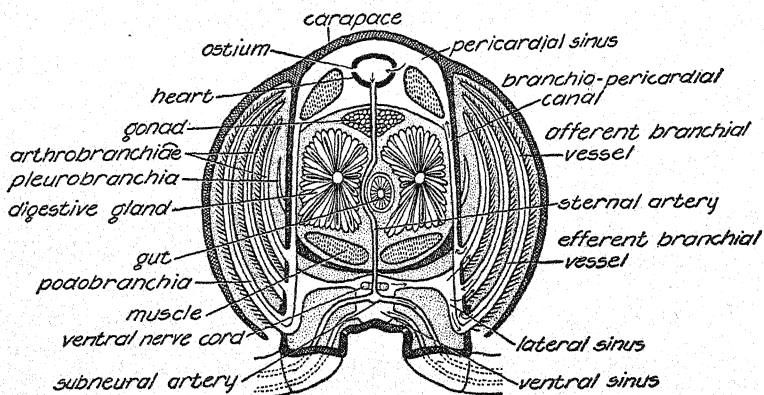


FIG. 349. The thoracic region of the crayfish, in cross section; the arrows show direction of blood flow (cf. Fig. 348).

extends anteriorly and posteriorly beneath the nerve cord. The anterior portion of the subneural artery, which is sometimes called the sternal artery, has branches to the esophagus, the oral appendages, and the three anterior pairs of pereopods. From the posterior portion of the subneural artery, which is also called the ventral abdominal artery, branches extend to the two posterior pairs of pereopods, the first pair of abdominal appendages, and the ventral abdominal muscles. The blood which passes from the heart in all these arteries is emptied from their branches into spaces between the cells throughout the body; there are no capillaries. From such spaces the blood is collected into the unpaired *ventral sinus* (sternal sinus) of the thorax, which communicates with the paired *lateral sinuses* by way of five pairs of small canals (Fig. 349). These lateral sinuses are in communication with the *afferent branchial vessels*, or sinuses of the gills, which are continuous with the *efferent branchial vessels* at the tips of the gill filaments. The blood, which has lost its carbon dioxide and gained oxygen in the gills, then passes dorsally through the six pairs

of *branchio-pericardial canals* to the pericardial sinus. When the heart expands, the blood is sucked into it through the ostia, which are guarded by valves. When the heart contracts, the blood is forced into the arteries to repeat its circulation, during which it distributes food absorbed from the digestive tract and oxygen absorbed through the walls of the gill filaments. In addition, excretions are collected from all regions and eliminated by way of the gills and green glands.

The *respiratory system* includes the *gills*, which are supplied with blood in the manner described (Fig. 349). In the living crayfish water is continually drawn under the ventral edges of the carapace into the gill cavities and, after passing over the gills, is expelled anteriorly by movements of the second maxillæ, which thus function in respiration as well as in feeding. The *excretory organs* are the pair of so-called *green glands*, which lie on each side anteriorly (Fig. 348). These glands are regarded as a single pair of greatly specialized nephridia, although they do not have internal openings leading from a cœlom as do the nephridia of annelids (cf. Fig. 335, p. 453). Since the green glands are richly supplied with arterial blood and lined in part by glandular epithelium, it is supposed that *excretion* occurs through the cells of this epithelium.

The Nervous System and Irritability. The *nervous system* occupies a position in relation to the digestive tract similar to its position in annelids (Fig. 350). There is a dorsal ganglionic mass, the *supra-esophageal ganglion*, or "brain," from which *nerves* pass to the eyes and antennæ, and from which the *circumesophageal connectives* extend to the *subesophageal ganglion* at the anterior end of the ventral nerve cord. From the subesophageal ganglion, nerves pass to the six pairs of oral appendages, as well as to the green glands, esophagus, and muscles of the anterior region of the thorax. During development there are six pairs of ganglia in this region in correspondence with the six pairs of appendages. The ventral nerve cord is a double structure composed of fused, paired ganglia and their connectives. Posterior to the subesophageal ganglion there is a pair of ganglia for each somite. The metameric structure of the animal is thus shown not only by the somites of the abdomen and the appendages throughout the length of the body but also by the nervous system. The make-up of the nervous system and its relative position are, therefore, comparable with what is found in the annelids (cf. p. 454).

In addition to the antennules and antennæ, which are *tactile organs*, the hairlike processes upon the appendages and other parts of the body, such as the edge of the carapace, are tactile in function. Related to these tactile structures are two *statocysts*, which are organs of equilibrium located upon the basal segments of each antennule. The stato-

cysts are saclike invaginations from the outer surface of the appendage; hence, they are lined with the exoskeleton, and the hairs that project into their cavities are comparable with the sensory hairs on other parts of the animal. Like the statocysts of other animals (*cf.* Fig. 301, p. 419), these organs contain particles called *statoliths*; but in the crayfish

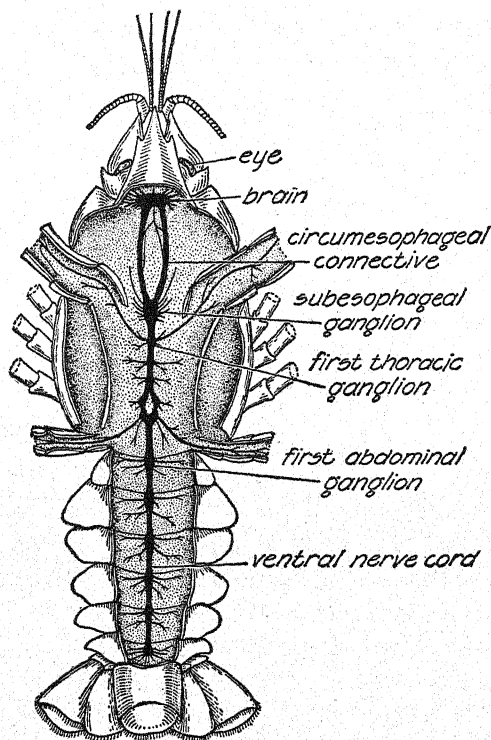


FIG. 350. Nervous system of the crayfish, *Astacus*, from dorsal view.

(Redrawn with modifications from W. Schmidt, 1915, *Zeitschrift für wissenschaftliche Zoologie*, vol. 113.)

the statoliths are foreign bodies, such as sand grains, and are lost at the time of molting. If a crayfish that has just molted is placed in water without such foreign particles, none can be found in the statocysts, and the animal will show a certain disturbance in the maintenance of its equilibrium. If iron filings are placed in the water, some of these may be worked into the statocysts, and the animal's reactions can then be tested by placing a magnet in different positions with reference to these organs. The reactions under such experiments indicate that the statocysts of the crayfish are organs of equilibrium,

in which the sensory hairs are stimulated by contact with the statoliths as the animal changes its position. In addition to these tactile and equilibratory sense organs, there are *chemoreceptors*, which can be stimulated by substances in solution and which are located on the antennules and probably on other parts of the body.

The Reproductive System, Reproduction, and Development. The sexes are separate. The *reproductive system* consists of *ovaries* or *testes*, each of which consists of paired anterior lobes and a median posterior lobe. These gonads lie dorsal to the digestive tract in the thoracic region, and their ducts pass ventrally (Fig. 349). The external openings of the *ductus deferentes* (vasa deferentia) are located on the basal segments of the fifth pereiopods; the openings of the *oviducts*, on the third pair of pereiopods. During sexual union spermatozoa are transferred from the male to a *seminal receptacle* on the ventral midline between the bases of the fourth pair of pereiopods of the female. As the eggs, which contain a relatively large amount of yolk, are laid, they are fertilized by sperm from the seminal receptacle and then attached to the swimmerets of the female. After hatching, the larvæ remain attached to the hairs of the swimmerets and develop through a series of molts until they have reached the stage of miniature adults and are able to begin an independent life upon the bottom (Figs. 345 and 351).

Other Crustacea. In an older classification, based upon less knowledge than is now available, the Class Crustacea was divided into only two subclasses, the *Entomostraca* and the *Malacostraca*. Such a grouping is still useful, inasmuch as it separates the crayfish and other highly developed types from those of simpler organization. It is true that many of the Entomostraca, like the water-flea, *Daphnia*, are greatly specialized; but some of them, like *Branchinecta*, are the simplest of all crustaceans in their metamerism and in the arrangement of their appendages (Fig. 352). Hence, one speaks of the Entomostraca as the "lower," and the Malacostraca as the "higher," Crustacea.

The Entomostraca. There are four principal types of Entomostraca, represented by the Orders Phyllopoda, Ostracoda, Copepoda, and Cirripedia. Like the Malacostraca, the majority of these crustaceans are marine, although the Phyllopoda are for the most part fresh-water animals. Among the Phyllopoda, which are known as the fairy shrimps, species of the Genus *Branchinecta* are representative (Fig. 352). The animal swims with the ventral surface uppermost by means of paddlelike thoracic appendages. The typical habitat is the shallow pools of fresh water that are formed by the spring rains and become dry later in the season. The males of *Branchinecta* are

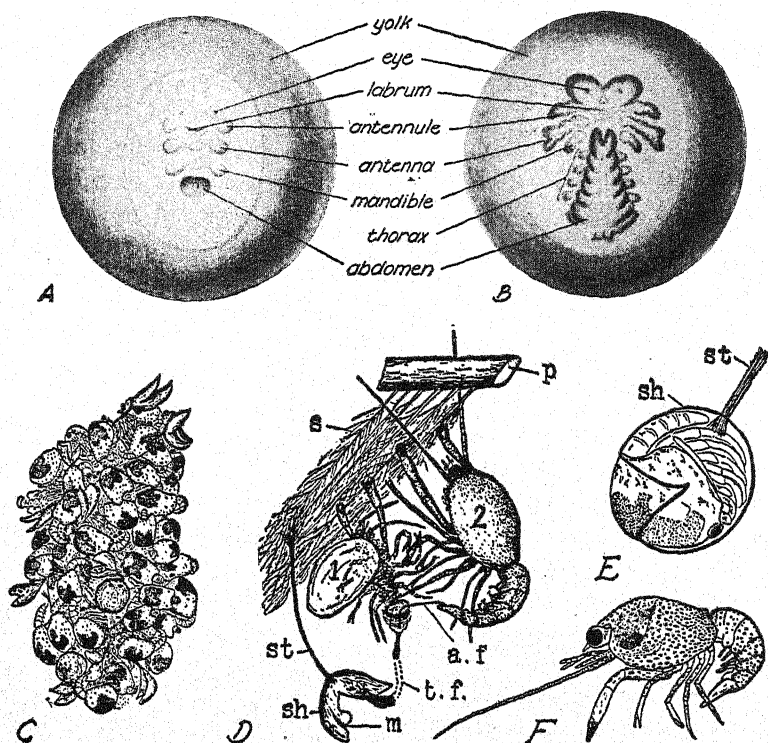


FIG. 351. Development of the crayfish. *A* and *B*, ventral view of eggs, showing early stages in development of the appendages and principal divisions of the body. *C*, mass of young crayfish upon a swimmeret of the mother (*cf.* Fig. 345). *D*, second larval stage (2) attached by its chelipeds to hairs (*s*) on a swimmeret (*p*) of the mother. The molted shell of first larval stage (1) is seen clinging by its chelipeds; the remains of egg-membrane (*m*) and eggshell (*sh*) are still attached to hairs of the swimmeret by a stalk (*st*). When the first larva hatches, it remains attached to the shell by a filament (*t. f.*) until its chelipeds can grasp a hair, and the second larva is similarly attached to molted shell of the first by a filament (*a. f.*). By means of these filaments the young remain fastened to the mother during periods of development when they might easily become detached. *E*, first larva hatching through a break in the eggshell (*sh*), which is attached to a swimmeret of the mother by a stalk (*st*). *F*, second larval stage.

(*A* and *B*, redrawn from G. B. Howes, "Atlas of zoöatomy," copyright, 1902, by Macmillan and Co., Ltd., printed by permission; *C* to *F*, after E. A. Andrews, 1916, Smithsonian Contributions, vol. 35.)

distinguishable by their second antennæ, which are modified as organs for clasping the females at the time of sexual union. The fertilized eggs are carried for a time in a brood-pouch on the ventral surface of the abdomen of the female. After the eggs become free, they can withstand drying and hence may be distributed like the encysted stages of Protozoa. Eventually, the young emerge as free-swimming larvæ, known as nauplii, with three pairs of appendages and a median eye. The adult arises from the *nauplius* by a series of molts, during which the characteristic features are gradually acquired.

The Cirripedia, or barnacles, represent an extreme modification in which the animal is attached during its adult life, although free-swimming in its larval stages. One type is the familiar rock-barnacle, *Balanus*, found between tide marks in the ocean; the other type, *Lepas*, is the "goose"-barnacle (Fig. 352 Below), so called because it was supposed by the naturalists of the Middle Ages to be the young of the wild goose. During its change from larva to adult the animal becomes attached by its anterior region. In the adult stage, as Huxley put it, the goose-barnacle "stands on its head and kicks its food into its mouth."

The Malacostraca. To these higher Crustacea belong the forms that are popularly known as the sow-bugs, scuds, shrimps, prawns, crayfishes, lobsters, and crabs (Fig. 353). Although the great majority are marine, many occur in fresh water; and a small number, like the sow-bugs and the land crabs of the tropics, are terrestrial. A few are parasitic upon larger animals. Since the number of somites and the division of the body into three principal regions are constant for all Malacostraca, a schematic representation of a malacostracan shows an animal essentially like a crayfish. The body is divided into head, thorax, and abdomen, which are composed of five, eight, and six somites, respectively, each bearing a pair of appendages; the telson is not considered to be a somite. The anterior part of the head bears the eyes, which are sense organs and not homologous with the appendages; posteriorly the abdomen terminates in a telson. A carapace, resembling that of the crayfish, may be present and is variously developed in different species. Although the internal organization is likewise modified in correlation with the habits of particular species, and the external features are highly specialized in many instances, the fundamental plan of structure remains the same.

The crabs are examples of a very specialized malacostracan. In the familiar "blue crab," *Callinectes sapidus* (Fig. 353 B), the eggs begin their development attached to the abdominal appendages of the female, as do the eggs of the lobster. Then there are pelagic larvæ, called *zoea*

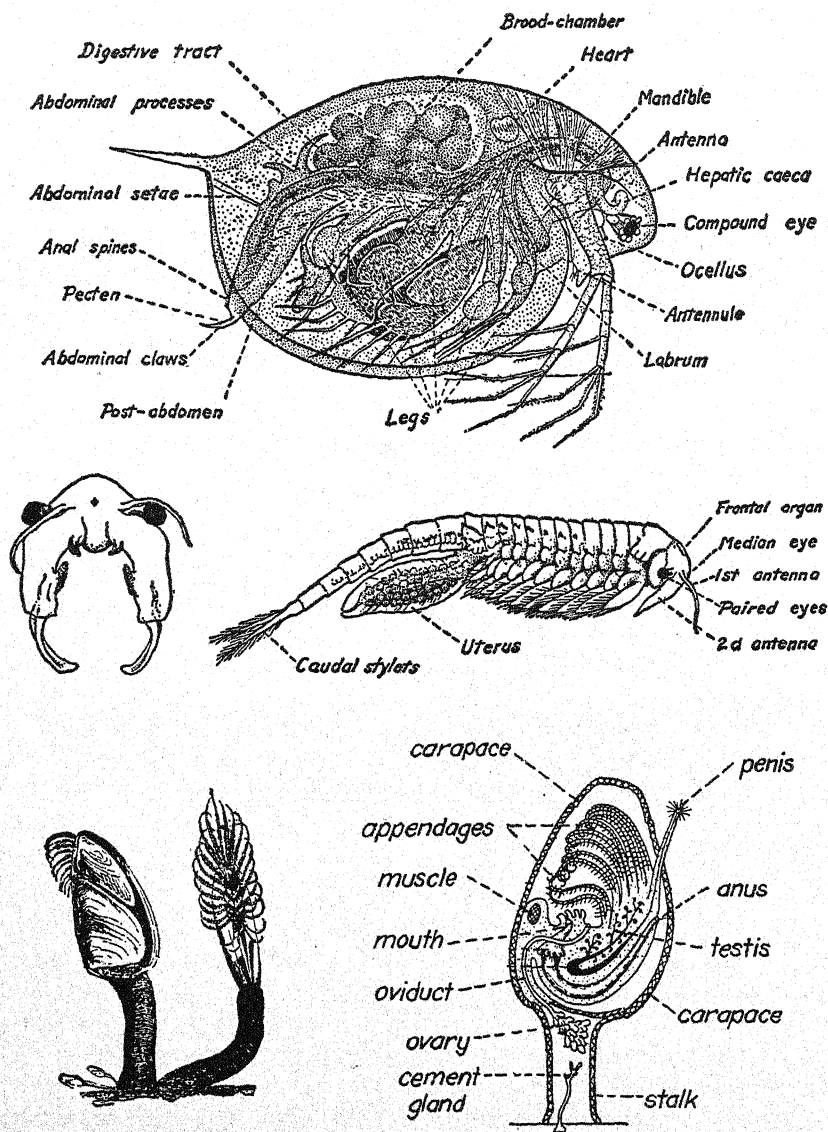


FIG. 352. Representative Entomostraca. Above, a water-flea, *Daphnia pulex*, one of the Cladocera. Middle, a fairy shrimp, *Branchinecta packardii*, one of the Phyllopoda; left, anterior view of a male showing the second antennæ modified as clasper organs; right, lateral view of a female showing appendages and the so-called uterus filled with eggs. Below, the goose barnacle *Lepas*, one of the Cirripedia; left, external features; right, internal structure.

(Above and Middle, from G. S. Dodds, 1915, University of Colorado Studies, vol. 11. Below, from W. Stempel, "Zoölogie im Grundriss, 1926.)

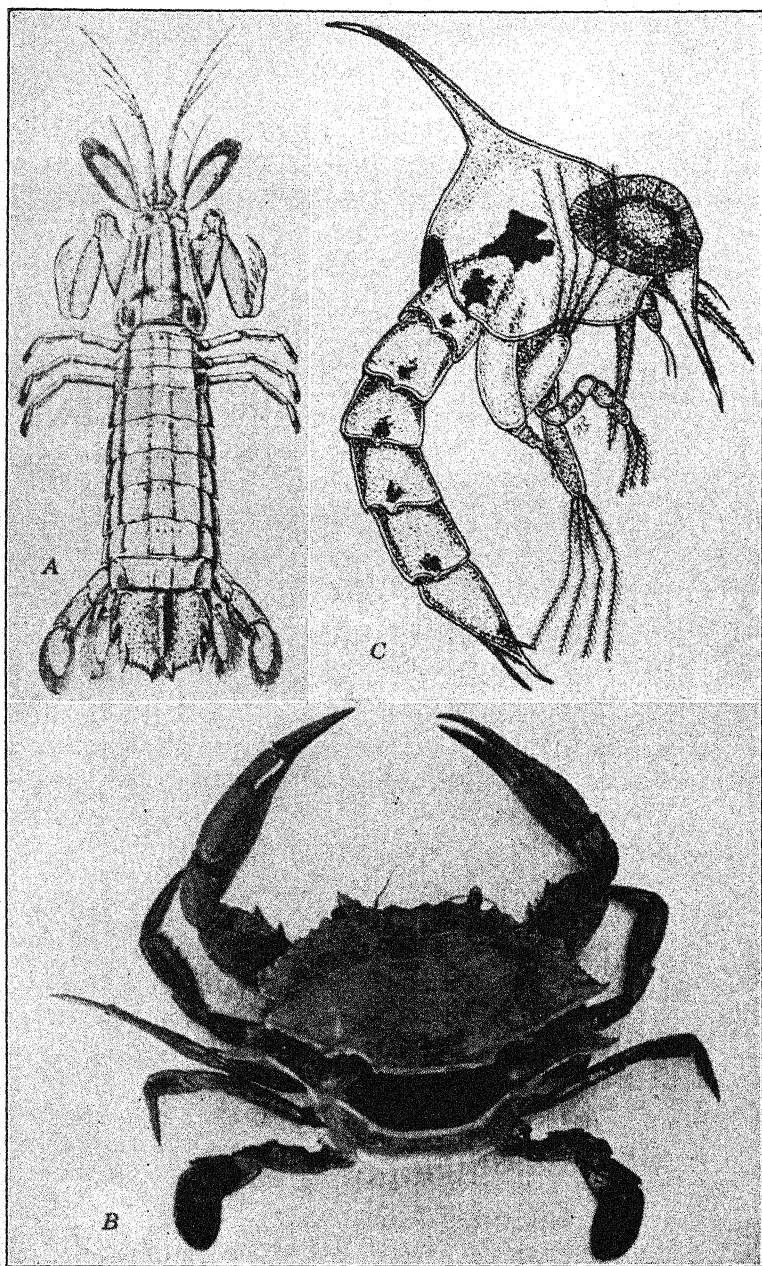


FIG. 353. Special examples of the Malacostraca. A, the mantis shrimp, *Chloridella (Squilla) empusa*. B, the blue crab, *Callinectes sapidus*, in process of molting (cf. Fig. 358). C, pelagic larval stage of blue crab, called the *zoea*.

(A, from F. C. Paulmier, Bulletin 91, Zoölogy 12, New York State Museum, 1905. B and C, from C. L. Newcombe, Educational Series, No. 4, Virginia Fisheries Laboratory, 1945.)

(Fig. 353 C), and later the larvæ, called *megalops* (cf. Fig. 347). In the metamorphosis to the adult the abdomen of the larva becomes tucked against the ventral side of the thorax and is relatively much smaller than in the lobster or crayfish. Figure 353 B shows the blue crab in process of molting, with its skeleton cracked open along the line between thorax and abdomen (cf. Fig. 358). The newly molted, or "soft-shelled" crab, is esteemed even more as a delicacy than the normal animal.

The mantis shrimp, *Chloridella* (*Squilla*) *empusa*, is another greatly specialized malacostracan (Fig. 353 A). It burrows into muddy bottoms in shallow water. The chelæ differ from those of the lobster and crayfish, and they are developed upon a different somite. The carapace is shorter than in the lobster, so that the five posterior somites of the thorax can be recognized dorsally. The powerful tail fin is used for burrowing as well as swimming. The gills are outgrowths from the abdominal appendages. Comparison of the mantis shrimp with the lobster and with the crab presents an interesting study in comparative anatomy.

The Insecta

In number of species the Insecta are today the dominant form of animal life upon the land. Few are marine, and the species that occur in fresh water are evidently forms descended from terrestrial ancestors in the manner of fresh-water snails (cf. p. 435). The most easily recognizable external features of insect structure are the division of the body into head, thorax, and abdomen; the two pairs of wings and three pairs of appendages upon the thorax; and the spiracles, which are the openings of the air-tubes, or tracheæ, which function in respiration. Representatives of the Order *Orthoptera*, which includes the locusts and grasshoppers, will be described to illustrate the structure and activities of insects in general; other orders will be discussed more briefly.

The Locust: *Habitat and Activities.* The words locust and grasshopper are frequently confused in scientific as well as popular speech. In the locusts the antennæ are relatively short, as in the common roadside locusts, whereas in the grasshoppers the antennæ are longer, as in the meadow grasshoppers and katydids. Unfortunately, the name locust has also been applied in the United States to an entirely different kind of insect, the cicada (Fig. 378). Since many species among the true locusts can be used for study, the account that follows is sufficiently general to be applicable to any one of the more common forms.

Locusts are universally distributed on all continents in climates where the insect life of open fields abounds. They crawl upon the grass and similar vegetation, leaping into the air by means of the posterior pair of legs and sustaining their flight according to the development of the wings. Their shrilling as they rest upon the ground and the clacking of their wings in flight are familiar sounds of the day, just as the notes of their near relatives, the katydids and crickets, are

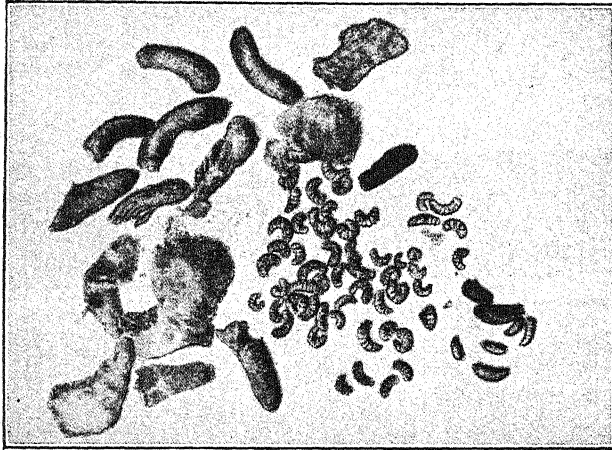


FIG. 354. Insect enemies of locusts. To the *left*, egg-masses of locusts are shown (*cf.* Fig. 369 B); to the *right*, larvæ of blister beetles (*cf.* Fig. 379) and of bee-flies found in the distorted remnants of egg-masses which appear as the larger bodies.

(From F. B. Milliken, 1920, Farmers' Bulletin, No. 691, U. S. Dept. Agriculture.)

among the most familiar sounds of night. Locusts may be grouped into non-migratory and migratory species. The common forms are non-migratory and may spend their entire lives within the radius of a single field. Individuals of the migratory type, of which the warrior locust, *Camnula pellucida*, and the lesser migratory locust, *Melanoplus mexicanus*, are now the most important, breed in one locality and migrate to another. Hatching occurs in May or June, depending upon the season, and migration begins within a few hours. The animals travel toward the sun as long as it shines. As the wings have not yet developed, locomotion at this stage is effected principally by crawling rapidly over the ground, although the air is filled with hopping individuals as the swarm moves forward. When they cross a cultivated field, the plants are eaten even to the roots, yet the swarm passes on

to what may be barren territory beyond, without destroying the growth that may stand on each side.

Both migratory and non-migratory locusts appear in varying numbers from year to year because of fluctuations in the abundance of their enemies and in the environmental conditions that are favorable to their development. Probably enough eggs are laid each year to

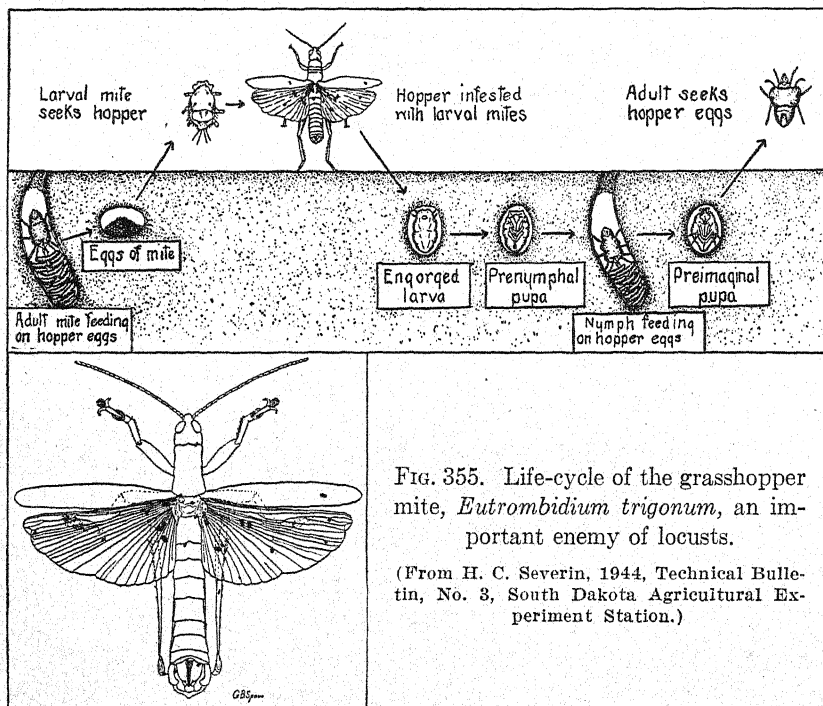


FIG. 355. Life-cycle of the grasshopper mite, *Eutrombidium trigonum*, an important enemy of locusts.

(From H. C. Severin, 1944, Technical Bulletin, No. 3, South Dakota Agricultural Experiment Station.)

produce a plague if they came to maturity, but this can occur only under exceptional conditions. Frequent freezings and thawings of the ground during the winter kill the eggs, and the young individuals die if the spring weather is cold and wet; in hot and dry weather, however, many eggs hatch and many young reach maturity. Many enemies, such as field-mice, ground-squirrels, moles, and skunks, dig for the eggs. Insectivorous birds, toads, lizards, snakes, and skunks devour large numbers of the young and adults. The larvæ of blister-beetles are by far the most important insect enemies (Fig. 354). These beetles lay their eggs in the ground, where they soon hatch into active larvæ which seek out the locust egg-masses and devour them. The larvæ of bee-flies are another enemy of the same sort, although less

important. Still another is an insect that lays its eggs with those of the locust; when the eggs of the parasite hatch, the young enter the eggs of the locust and develop at their expense. Other insect parasites, such as the young of certain flies that have laid their eggs upon the bodies or wings of the locust, are often found in the fat body, into

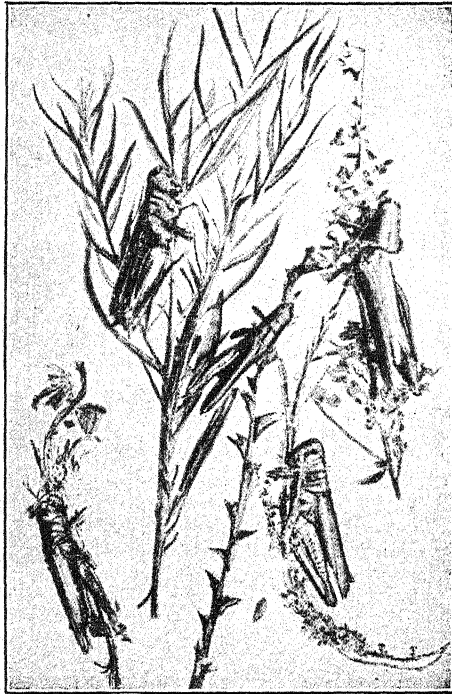


FIG. 356. Locusts killed by a fungous disease.

(From H. C. Severin and G. I. Gilbertson, 1917, Bulletin No. 172, South Dakota Agricultural Experiment Station.)

which the parasites bore after hatching (*cf.* Fig. 383). Here they feed until they are ready to transform into adults; they then make their way to the outside, thereby killing the locust. Mites are also serious enemies (Fig. 355). And fungous diseases are often epidemic among locusts, destroying large numbers of the young and adults (Fig. 356).

General Structure. Division of the body into *head*, *thorax*, and *abdomen* is conspicuous in the locust (Fig. 357). Metamerism is obvious in the abdominal region, in which ten somites can be recognized. There are three thoracic somites, the prothorax, mesothorax, and metathorax, as indicated by the three pairs of legs. Although the

number in the head is problematical, there is clear evidence of four somites. The *skeleton*, like that of other arthropods, is a firm covering which is thinner in some regions but everywhere continuous over the outer surface and extends into the anterior and posterior ends of the digestive tract, as in the crayfish (cf. p. 472). Unlike the skeletons

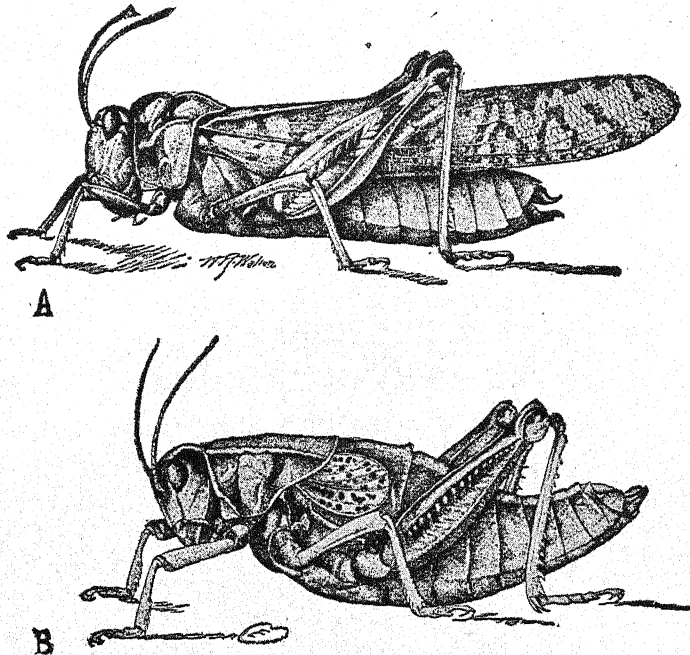


FIG. 357. Representative locusts. A, the New Mexico long-winged locust, *Disosteira longipennis*; adult female, enlarged about one-third. B, the south-western lubber locust, *Brachystola magna*; adult female, natural size.

(From W. R. Walton, 1922, Farmers' Bulletin, No. 747, U. S. Dept. Agriculture.)

of many crustaceans, the chitinous skeleton of the locust and other insects is not hardened with carbonate of lime. As in the crustaceans and all other arthropods, a new skeleton is secreted by the underlying epidermal cells before each molt and without becoming attached to the old skeleton (Fig. 358).

The *appendages* of the head consist of a pair of sense organs, the *antennæ*, and three pairs of oral appendages or mouthparts. The two *compound eyes* and the three simple eyes, or *ocelli*, are primarily sense organs, and not appendages modified for sensory functions, as the antennæ may be. What are called the mouthparts of the locust include an upper lip, or *labrum*, which is not formed by the fusion of

right and left appendages, as might be supposed; a pair of appendages known as the *mandibles*, which are the jaws on each side of the mouth;

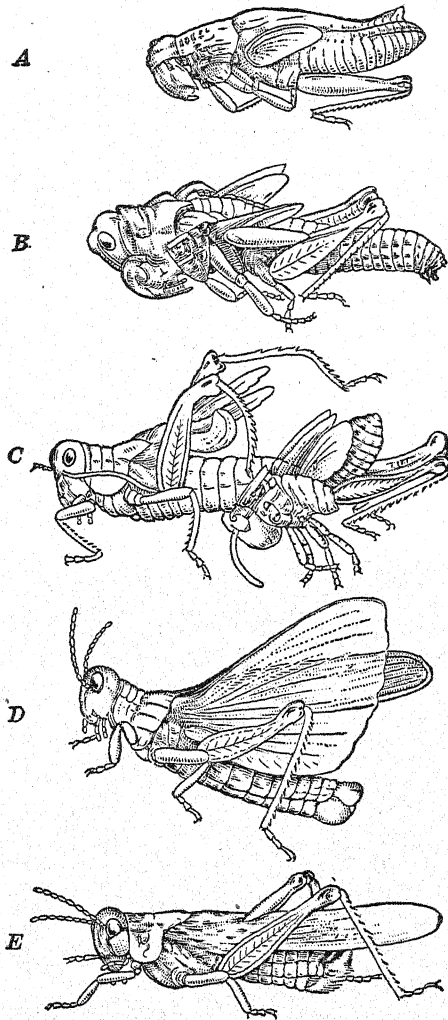


FIG. 358. Molting of a locust. A-E, successive stages in the process.

(After C. V. Riley, from H. R. Linville and H. A. Kelly, "General zoölogy," copyright, 1906, by Ginn and Co., reprinted by permission.)

a tongue-like projection, the *hypopharynx*, which, like the labrum, is a single median structure and not a fused pair of appendages; the *first maxillæ*, which are clearly paired appendages; and the *labium*, which functions as a lower lip, although, unlike the labrum, it is formed

by fusion of a pair of appendages, the *second maxillæ* (cf. Figs. 359 and 360). The mouthparts thus include two median structures, which are not appendages, and three pairs of appendages. These mouthparts are referred to as *mandibulate* because of the mandibles, which are used for biting and chewing. The three pairs of thoracic appendages, or *legs*, are jointed and similar in structure, although the most

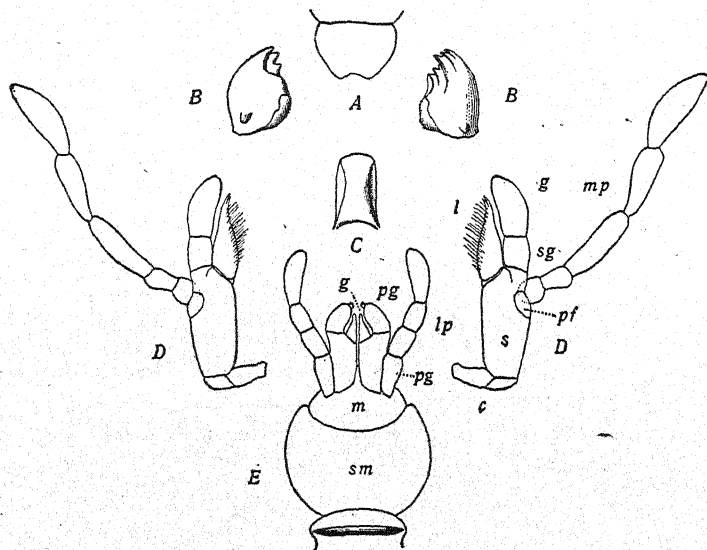


FIG. 359. Mouthparts of a cockroach, *Ischnoptera pennsylvanica*. Mouthparts of insects show great diversity of structure in relation to feeding habits. All seem to have evolved from the simpler mandibulate types with jaws and other parts, such as are found in cockroaches and locusts. A, labrum. B, mandibles. C, hypopharynx. D, first maxillæ, each with basal portions (s and c), lacinia (l), galea (g and sg), and palp (mp and pf). E, labium, or fused second maxillæ, with basal portions (sm and m), glossa (g and pg) and palps (lp).

(From J. W. Folsom, "Entomology," copyright, 1906, by P. Blakiston's Son and Co., reprinted by permission.)

posterior pair is specialized for jumping. A minute pad and a pair of hooks at the distal end of each leg provide grasping organs by which the animal secures a firmer hold upon the vegetation. The abdomen is devoid of appendages, and none appears in this region during development, although there are traces of such vestigial abdominal appendages in the development of certain insects and in the adult stage of some wingless forms. The posterior end of the abdomen differs in the two sexes, principally because of the presence in the female of the large

ovipositor, within which lies the opening of the female reproductive duct (Figs. 357 A and 369 A). In the male there is a thick, conical copulatory organ, or *penis*, located between the anus and the external genital opening on the terminal segments of the abdomen.

Two pairs of *wings* are attached to the dorso-lateral surfaces of the mesothoracic and metathoracic somites, as they are in the majority of insects. In some species of locusts, the anterior wings are heavy and function as wingcovers. In the lubber locusts, both pairs of wings are greatly reduced, with a corresponding decrease in the power of flight (*cf.* Fig. 357 A and B). The wings of insects are composed mainly of exoskeleton with a very small amount of other material between the two layers. They are stiffened by thickened portions, called "veins," between which the wing is thin and membranous.

The external openings of the *respiratory system* appear as the paired *spiracles* on each side of the three thoracic segments and on the eight anterior abdominal segments (Fig. 361). The number of spiracles differs in insects, but typically there is a pair for each somite of the thorax and abdomen. In life they open and close rhythmically with the respiratory movements of the body. The *tympanic membranes*, which are the external parts of the auditory organs, are conspicuous structures on the dorsal portion of the first abdominal somite (Fig. 361 C).

Structures and Functions Related to Metabolism. The internal structure is much the same in all species of locusts. The following account is applicable in general to any of the common species, but particularly to the Carolina locust, *Dissosteira carolina*. In the *digestive system* the mouthparts, which have been described in connection with the appendages, surround the *buccal cavity* (Fig. 360). Opening into this buccal cavity, on the anterior face of the labium, is the duct from the *salivary glands*, which are located in the thorax. From the buccal cavity a short *esophagus* passes dorsally to a large, thin-walled *crop* that extends into the thorax and tapers before entering the next region of the tract, which is called the *stomach*. The transition from crop to stomach is marked by six glandular outgrowths of the tract, which are known as the *gastric cæca* and secrete a digestive juice (Fig. 361 B). The stomach is followed by the *intestine*, which has a narrow region, called the colon, near the middle, and an expanded posterior part, called the rectum, which leads to the *anus*. The division between stomach and intestine is marked by the entrance of the Malpighian tubules (*cf.* p. 492).

In feeding, the animal bites off pieces of grass or other vegetation with its mandibles, using the labrum and labium as upper and lower

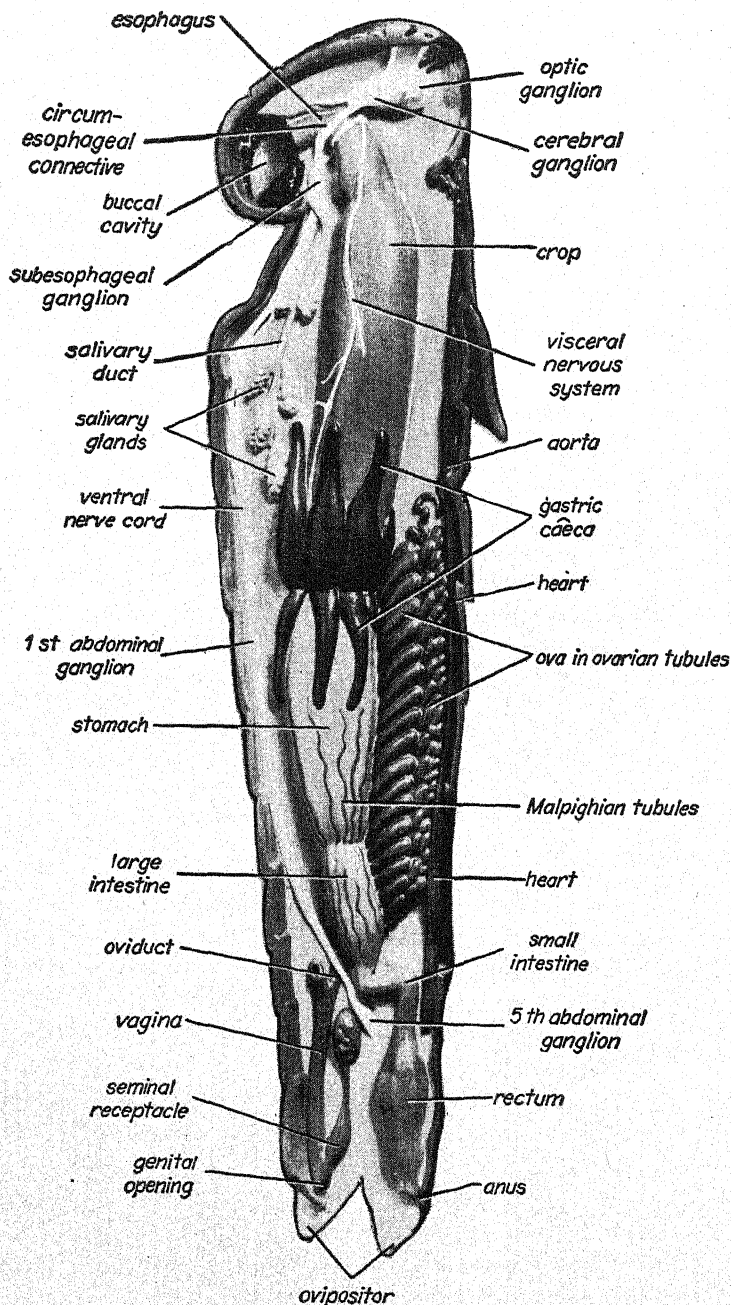


FIG. 360. Internal structure of a locust.

(From photograph of a Jewell Model. Courtesy of F. M. Jewell, Carlinville, Illinois.)

lips, respectively, and the maxillary and labial palps as tactile organs. The salivary secretion, which is emptied into the buccal cavity, serves as a lubricant in swallowing and as a digestive fluid after the food has reached the crop. As its name implies, the crop functions principally for storage. *Digestion* may occur in its posterior end, but the cavity of the stomach is the principal region of digestion. The so-called "mo-

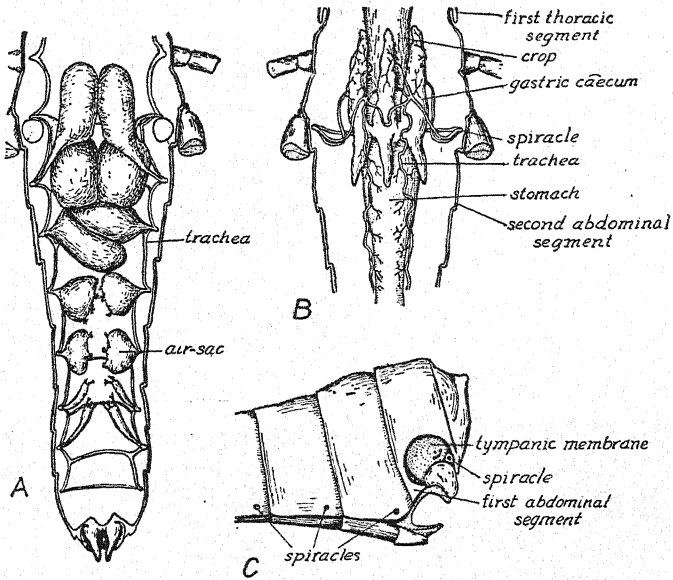


FIG. 361. Respiratory system of the locust, *Dissosteira carolina*. A, air-sacs and tracheae of the abdomen, dorsal view. B, branching of tracheae on the digestive tract. C, spiracles on the abdomen, lateral view.

(From R. E. Snodgrass, 1903, Educational Publications, No. 2, Washington Agricultural College.)

lasses" that is extruded from the mouth when a living locust is handled is the contents of these anterior portions of the digestive tract mingled with the digestive fluid of the gastric cæca. *Absorption* is the passage of the products of digestion through the wall of the digestive tract into the blood in the surrounding hemocel. The distribution of absorbed food and its diffusion into the cells make *assimilation* possible.

As in the crayfish, the *cœlom* is problematical, although it is probably represented by certain rudimentary cavities. The spaces between muscles and other mesodermal parts are hemocels (*cf.* p. 216) and do not represent a degenerate *cœlom*. In the adult locust this region is largely occupied by an irregular mass of storage tissue called the *fat-*

body. Such a fat-body constitutes the greater bulk of the body in insect larvæ that store food in advance of metamorphosis. Parasites that invade the bodies of insects feed principally upon this accumulated food.

The spiracles, which are the external openings of the *respiratory system*, occur on the thoracic and abdominal somites. Leading from

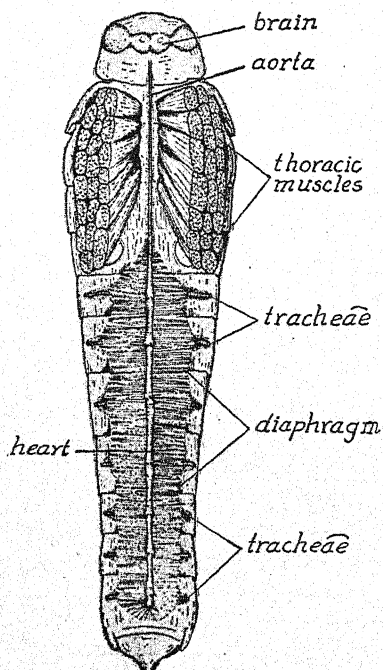


FIG. 362. Heart of the locust, *Disosteira*, ventral view.

(From R. E. Snodgrass, *op. cit.*)

the spiracles are the air-tubes, or *tracheæ*, which unite and branch in a complex manner and expand into conspicuous reservoirs, or *air-sacs*, in the abdominal region (Fig. 361). The fine subdivisions of the tracheæ end blindly in all parts of the body and make possible a direct delivery of atmospheric oxygen to all cells. *External respiration* occurs by way of the spiracles, a fact which makes it possible to kill insects by clogging these openings with dust or films of oil or soapsuds. *Internal respiration* results from the diffusion of oxygen from the tracheæ into the cells. The tracheæ also serve to connect and bind together parts of the insect's body, and, correlated with this relationship, there is relatively little connective tissue. That this type of respiratory system, which is unique in the Arthropoda and most highly developed in the insects, is extremely efficient is indi-

cated by the fact that many insects are capable of rapid and sustained metabolism.

The *Malpighian tubules* are regarded as the *excretory organs* of insects. Each tubule is composed of large cells surrounding a cavity and enclosed by an epithelium. The lumen of the tubule communicates with the cavity of the intestine. The tubules end blindly at their free ends, which extend into the hemocœl, where they are surrounded by the blood. It is supposed that excretory substances pass from the blood through the cells into the cavities of the tubules and thence to the intestine. The excretory function is further indicated

by the relatively large amounts of nitrogenous material that can be detected in the Malpighian tubules by chemical tests.

Since the *circulatory system* is not concerned with the delivery of oxygen, it is not surprising to find that this system is not extensively developed and that the flow of blood is very sluggish. The *heart* of the locust is a slender, pulsatile tube extending along the dorsal midline in the abdomen and having a pair of *ostia* for each somite throughout its length (Fig. 362). Ventral to the heart is the *pericardial sinus*, which is a space that is partially separated from the remainder of the hemocoel by a membrane sometimes called the *diaphragm*. Blood enters the heart through the ostia and is driven anteriorly into the thorax and head, through the *aorta*, which is an extension of the heart (cf. Fig. 363). From the aorta the blood enters the general cavity of the hemocoel and flows posteriorly to the abdomen, where it again enters the pericardial sinus and the heart. There are white cells in the blood of locusts, but no colored cells comparable with the red blood cells of vertebrates.

The Nervous System and Irritability. The *nervous system*, like that of the crayfish and other arthropods, consists of a dorsal ganglionic mass, the *supraesophageal ganglion*, sometimes called the "brain," *circumesophageal connectives*, and a ventral *nerve cord* composed of a series of paired ganglia and their connectives (Figs. 360 and 364). In the Carolina locust the brain, which lies in the head between the compound eyes, has three parts indicative of its origin by the fusion of three pairs of ganglia during development. Nerves pass from the brain to the three ocelli, to the antennæ, and to the labrum. In addition, small nerves extend ventrally to the *frontal ganglion*, from which the visceral, or sympathetic, nerve leads to the anterior part of the digestive tract. The circumesophageal connectives lead to the sub-

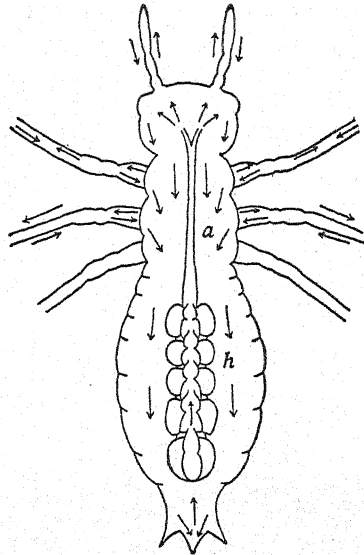


FIG. 363. Course of circulation in the larva of a dragon-fly, *Epiptera*. The flow of blood through the five-parted heart (*h*) and the aorta (*a*), and its course through the hemocoels, as shown by the arrows, can be seen in the living animal.

(After H. J. Kolbe, from J. W. Folsom, "Entomology," copyright, 1906, by P. Blakiston's Son and Co., reprinted by permission.)

esophageal ganglion. The subesophageal ganglion, which originates from three pairs of ganglia during development, is a single median mass in the adult and sends nerves to the mandibles and to the first and second maxillæ. In the thorax there are three pairs of ganglia, corresponding to the three thoracic somites, but the posterior pair of these ganglia is larger, and its nerves are distributed in such a way as to indicate its origin by fusion of the third thoracic and the first abdominal pairs of ganglia. In the abdomen there are five pairs of ganglia, but these represent fusions, particularly at the posterior end of the ventral

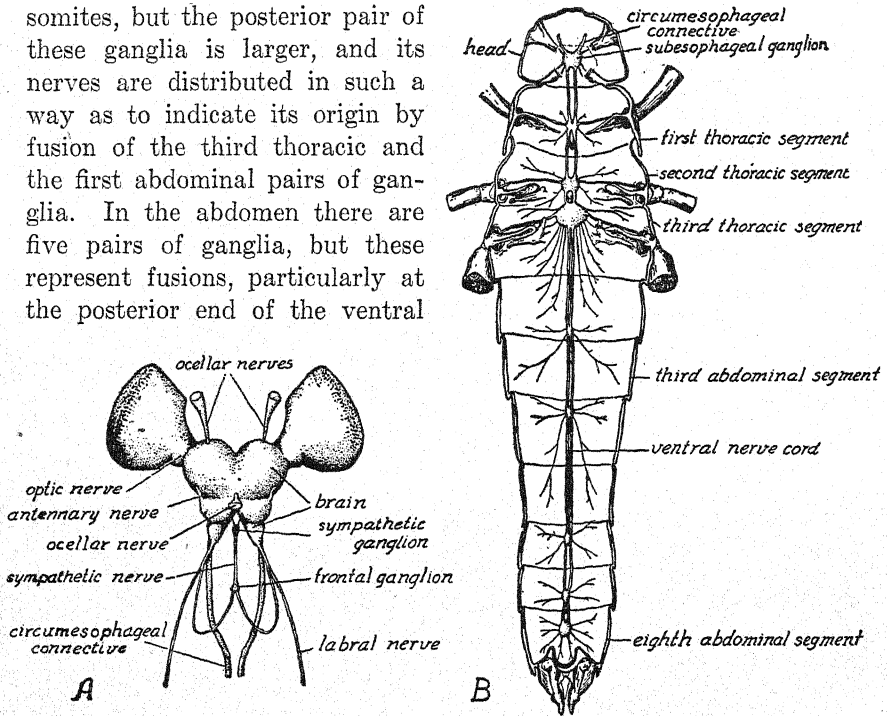


FIG. 364. Nervous system of the locust, *Dissosteira carolina*. A, anterior parts, cephalic view (cf. Fig. 360); drawn on a larger scale than B. B, ventral nerve cord, dorsal view.

(From R. E. Snodgrass, 1903, Educational Publications, No. 2, Washington Agricultural College.)

nerve cord. The adult locust, therefore, has fewer ganglia than somites, but in the embryo there is a pair of ganglia for each somite, as in the less-specialized arthropods.

Locusts, like the majority of insects, are well equipped with *sense organs*. The entire outer surface is sensitive to tactile stimuli, and there are special tactile organs or areas, such as the antennæ, the cerci at the posterior end of the abdomen, some of the mouthparts, and the distal segments of the legs, which are particularly sensitive (Fig. 365 Left). Although these organs are primarily tactile, olfactory stimuli

affect the basal parts of the antennæ, as may be demonstrated by experiments in which the parts concerned are coated with paraffin (Fig. 365 Right). Some insects must be able to respond to very slight olfactory stimuli. For example, the males of certain moths will come up against the wind from long distances in search of the females.

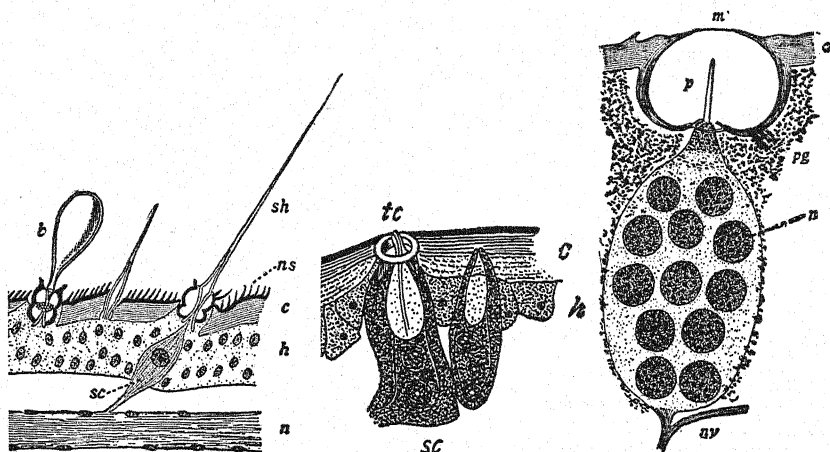


FIG. 365. Sense organs of insects. *Left*, longitudinal section of portion of a caudal cercus of the cricket, *Gryllus domesticus*, showing a type of hair (*sh*), presumably tactile in function, at the base of which, in the epidermis (*h*), is a sensory cell (*sc*), from which nerve fibers pass to a nerve (*n*); another type of hair (*b*), which is bladderlike and small non-sensory hairs (*ns*) extending from the cuticle (*c*) are also shown. *Center*, section through an organ of taste of an insect, showing the taste cup (*tc*) at the surface of the cuticle (*c*); beneath the epidermis (*h*) at the base of the taste organ are sensory cells (*sc*). *Right*, olfactory sense organ from the antenna of the grasshopper, *Coloptenus*; a cell with many nuclei (*n*) is prolonged into a bristle lying in a pit (*p*) which has a thin membranous external covering (*m*); nerve fibers (*nv*) occur at the base of the cell; pigment granules (*pg*) are shown in the epidermis beneath the cuticle (*c*).

(*Left*, after O. vom Rath; *center*, after F. Will; *right*, after G. Hauser; from J. W. Folsom, "Entomology," copyright, 1906, by P. Blakiston's Son and Co., reprinted by permission.)

Gustatory stimuli probably affect taste organs known to occur upon the mouthparts of the locust (Fig. 365, Center). The ocelli, or simple eyes, are probably incapable of forming images and hence are organs of light perception only (*cf.* Fig. 366 C). When the compound eyes are coated with black paint, the animal will not react to moving objects by leaping away, but it will find its way out of a box in which there is only one small opening that admits light. When the ocelli,

as well as the compound eyes, are painted, the insect does not find such an opening except by chance. It has been shown that some insects respond differently to different colors, although the range of stimulation may not be the same as that in man. Ants, for example, will avoid violet light, as they will direct sunlight, and they seem not to

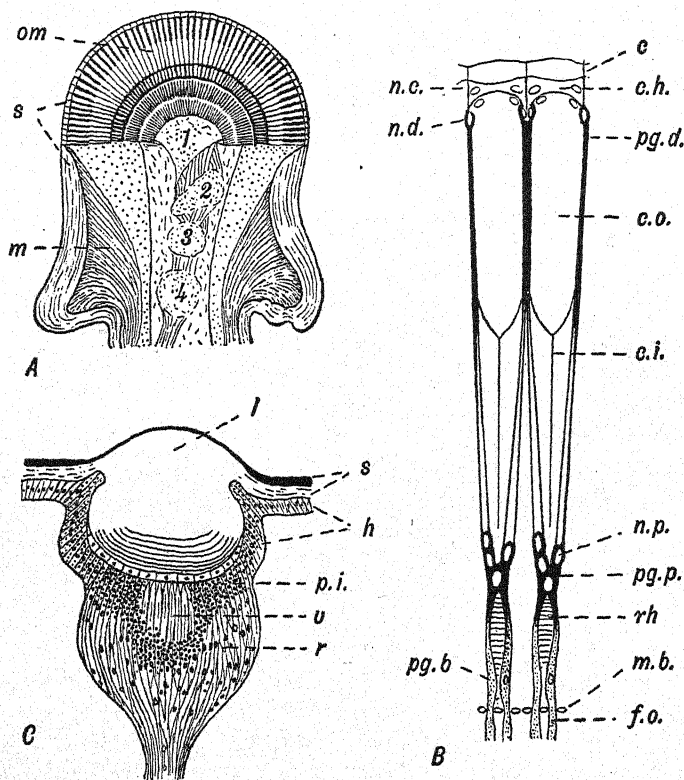


FIG. 366. Eyes of arthropods. A, compound eye of the crayfish, in longitudinal section, showing the numerous ommatidia. B, two ommatidia of the crayfish, showing details of structure. C, ocellus or simple eye of the honey-bee, in longitudinal section. 1, 2, 3, and 4, optic ganglia; c, corneal facet, or external surface of ommatidium; c. h., epidermis cells of facet; c. i., crystalline cone, proximal part; c. o., crystalline cone, distal part; f. o., fibers of optic nerve; h, epidermis; l, lens; m, muscle; m. b., basal membrane; n. c., nucleus of corneal cell; n. d. and n. p., nuclei of retinal cells; om, ommatidium; pg. b., pg. d., and pg. p., pigment; p. i., pigment of iris; r, retinal cells; rh, rhabdome; s, skeleton; v, vitreous body.

(A and B redrawn from G. B. Howes, "Atlas of zoöatomy," copyright, 1902, Macmillan and Co., Ltd., printed by permission; C, redrawn from J. W. Folsom, *op. cit.*, printed by permission.)

distinguish red or orange light from darkness. Again, ants and honeybees are very sensitive to ultraviolet light, to which man gives no conscious responses. Each compound eye consists of many units, the *ommatidia*, which are similar in structure and so arranged that the axis of each is perpendicular to the curved surface of the eye,

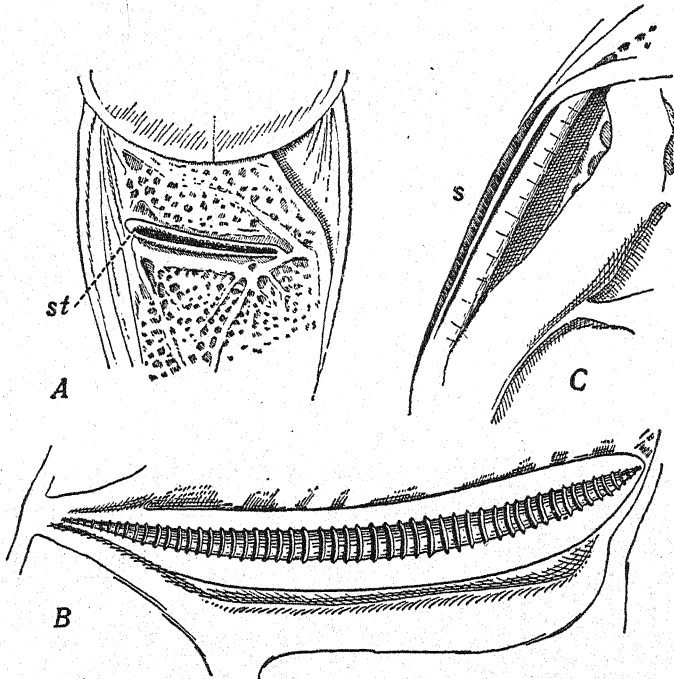


FIG. 367. Stridulating organs of the katydid, *Microcentrum laurifolium*. A, dorsal aspect of the file (*st*) when wingcovers are closed. B, ventral aspect of left wingcover to show the file. C, dorsal aspect of right wingcover to show the scraper (*s*).

(From J. W. Folsom, *op. cit.*, reprinted by permission.)

where the outer end of the ommatidium is exposed (*cf.* Fig. 366 A and B). What an insect sees is apparently the result of the combined contributions of the separate ommatidia, each one being stimulated by the intensity and color of light in the path of its longitudinal axis. The image is consequently made up in the manner of a mosaic, rather than being seen as a whole, as through the eyes of vertebrates. An eye of this sort seems especially fitted to perceive moving objects, which stimulate different ommatidia in succession.

Sound production and sound perception are commonly correlated in

animals. Thus, almost every insect that makes definite sounds possesses structures that can be regarded as auditory organs, although it may be difficult to ascertain just how the sounds are produced and where the auditory organs are located. The "song" and the auditory organs of the katydid (Figs. 367, 368, and 375) represent a familiar example of this correlation between sound-producing and sound-receiving organs.

In addition to sounds produced when the insect is at rest are the "flight songs" of many locusts. It has long been assumed, despite accounts to the contrary, that these sounds were produced by rubbing

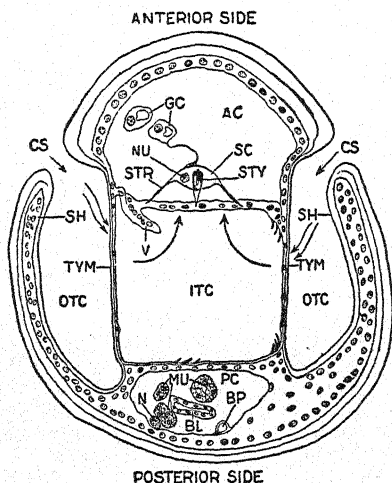


FIG. 368. Diagrammatic transverse section through anterior thoracic appendage of the katydid, *Microcentrum rhombifolium*, showing structure of the organ of hearing (cf. Fig. 374). The two outer tympanic chambers (OTC) are covered by folds (SH) of the wall of leg and communicate with the outside by slits (CS); they are separated by the tympana or drums (TYM) from the inner tympanic cavity (ITC), which is a modification of a trachea. A membrane (V) separates the anterior chamber (AC) from the cavity (ITC), and a similar membrane is found separating the posterior chamber (PC). Vibrations in the air pass through the outer tympanic chambers and beat upon the tympana, setting up vibrations of the air in the internal tympanic cavity. These stimulate the sensory cell (SC), which has a nucleus (NU), a sensory process (STY), and supporting processes (STR) that attach it to the membrane of the anterior chamber. Impulses are set up and pass by nerve fibers to ganglion cells (GC), which transmit them to the central nervous system. In the posterior chamber are found muscles (MU), a nerve (N), a blood vessel (BL), and a trachea (BP).

(From U. Dahlgren, 1925, *Natural History*, vol. 25, courtesy of American Museum of Natural History.)

together the upper surface of the front edge of the wings and the lower surface of the wingcovers. Recent experiments in removing the wingcovers show that these organs are not concerned, since the characteristic sounds of flight are still produced. These sounds come from the hind wings, supposedly from the partial slackening of the membrane between the veins followed by sudden expansion. It also appears that other individuals of the species react to, and so "hear," the flight song. In the locust the tympanic membranes are assumed to be auditory organs, more on account of their structure than from any experimental evidence; they consist of a membrane against the inner side of which are structures connected with nerves (*cf.* Fig. 35, p. 66). In mosquitoes certain hairs on the antennæ of the male are regarded as auditory. It is supposed that in finding a mate the male mosquito adjusts its flight so that the two antennæ are stimulated alike by the wing-tones of a female.

In addition to the organs enumerated, other structures in insects are presumed to be sense organs because of their structure and connections with the nervous system.

The most conspicuous anatomical feature of the neuro-sensory mechanism in the insects is the degree of cephalization, or concentration of sense organs and ganglia with their adjustor nerve cells toward the head or cephalic end. This fact is obviously correlated with the very active life of most insects, which subjects them to frequent and varied changes in their environments, and resembles the more pronounced cephalization that characterizes the vertebrates. In like manner insects exhibit reflex actions of great complexity, involving what have been called chain reflexes in the vertebrates (*cf.* p. 73). Many of the activities to be mentioned in discussing other groups of insects will illustrate this statement. There is scant evidence that insects have any capacity comparable to the intelligence of higher vertebrates, although they instinctively perform very involved actions, especially in connection with mating, care of young, and colonial life.

The Reproductive System, Reproduction, and Development. In the account of external features, reference has been made to the differences between males and females. In the male there are two *testes*, which occupy a position dorsal to the intestine. The tubules of the testes open into right and left *ductus deferentes* (vasa deferentia), which unite as an *ejaculatory duct* leading to the penis. *Accessory glands*, which communicate with the anterior end of the ejaculatory duct, secrete a fluid that is apparently necessary in the transfer of the spermatozoa from male to female during sexual union. In the female there are two *ovaries* composed of cords in which the ova are formed. The

paired *oviducts*, with which these ovarian cords are connected on each side, unite in a median ventral portion, the *vagina* (Fig. 360). A tubular *seminal receptacle* opens within the space enclosed by the ovipositor, and the spermatozoa received at the time of sexual union are

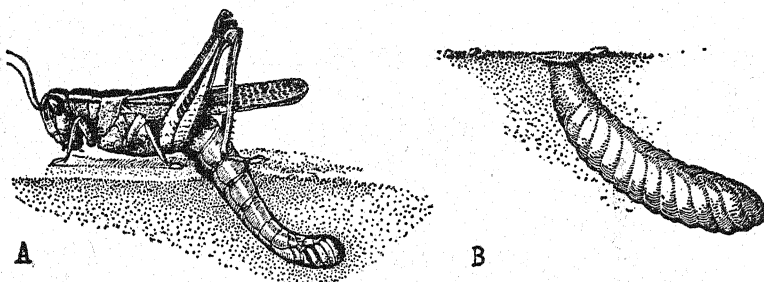


FIG. 369. Egg-laying of the locust. *A*, locust laying eggs. *B*, egg-mass in the ground.

(From W. R. Walton, 1922, *Farmers' Bulletin*, No. 747, U. S. Dept. Agriculture.)

stored within this receptacle until used for fertilization at the time of egg-laying. In egg-laying, the ovipositor is thrust into the ground and expanded to form a cavity, in which a mass of eggs is laid (Fig. 369 and *cf.* Fig. 370). With the withdrawal of the ovipositor and the

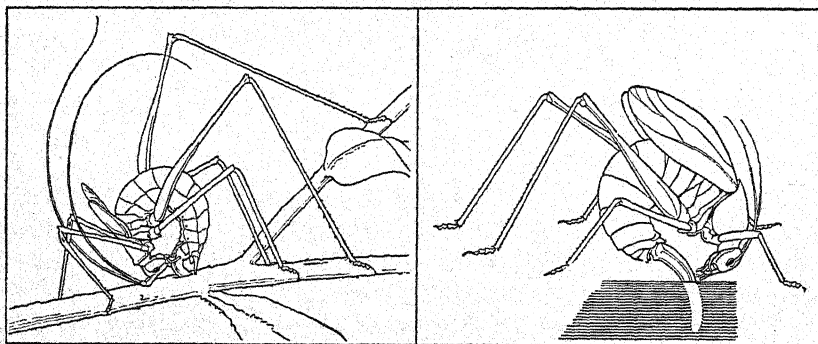


FIG. 370. Egg-laying of grasshoppers. The ovipositor is knifelike and used to pierce the stems of plants within which the eggs are laid. *Left*, *Arethæa ambulator*. *Right*, *Amblycorypha parvipennis*.

(From F. B. Isely, 1941, *Ecological Monographs*, vol. 11. Drawn by Ruth M. Sanders.)

collapse of the edges of the excavation, this egg-mass is left buried just below the surface. In temperate climates, most species of locusts lay their eggs during late summer and autumn, and the eggs do not hatch until spring. At the time of hatching, the young locust resembles

the adult, although the head is relatively larger and the wings have not yet appeared. The final size and proportions are reached by a series of molts (Fig. 371).

If the life-cycles of insects are examined, three types can be distinguished, although intergradations occur. In one the young individual that hatches from the egg resembles the adult except in size. In this life-cycle there is *direct development* and no metamorphosis, or fundamental change of structure, as the young insect reaches the adult size by a process of growth. In a second type of life-cycle, which is illustrated by the locust, the young which hatch resemble the adult in many respects but differ in certain ways, notably the absence of wings. The *nymph*, as it is called, feeds, grows, undergoes a series of molts, and gradually assumes all the adult characters. Fully differentiated wings appear at the final molt, and the individual is then an adult. No cessation of activity marks this life-cycle, which is called development with *incomplete metamorphosis*. In the third type of life-cycle, the young insect when it hatches bears almost no resemblance to the adult and is called a *larva*. The larva feeds and grows with frequent molts but does not change its structure. Eventually the larva ceases its activity and molts to form a *pupa*, which resembles the adult more than the larva. The pupa does not feed and remains quiescent while it undergoes a rather complete reorganization or *metamorphosis*. When the pupal skeleton is shed, the adult emerges and no further growth or structural changes occur. Such a life-cycle is called *indirect development*, because of the larval and pupal stages, and *complete metamorphosis*, because the larva changes so markedly to become the adult. In the accounts of other insects which follow, examples of these types of life-cycles will be noted.

Other Insecta. Opinion differs as to the number of orders into which this class of the Arthropoda should be divided. The twenty-one orders that follow represent one of the recognized classifications. Such a grouping expresses the opinion of certain investigators concerning the differences that are sufficient to justify a separation of types. It will be noted that the kind of life-cycle, the nature of the wings, and the differentiation of the mouthparts for biting (mandibulate) or sucking (suctorial) are the features most commonly used in this classification. The number of species stated for each order represents approximately the number thus far described.

A comparison of the various orders indicates that the more generalized types of insects possess mandibulate mouthparts and that those orders in which the mouthparts are modified for sucking possess mandibles in their larval stages. In the simplest insects (Thysanura and

Collembola) wings are absent in the larval as well as in the adult stages. In other insects that are wingless as adults, the presence of wing rudiments in the larvæ indicates that two pairs of wings are characteristic of the great majority of insects. The specialization of the anterior

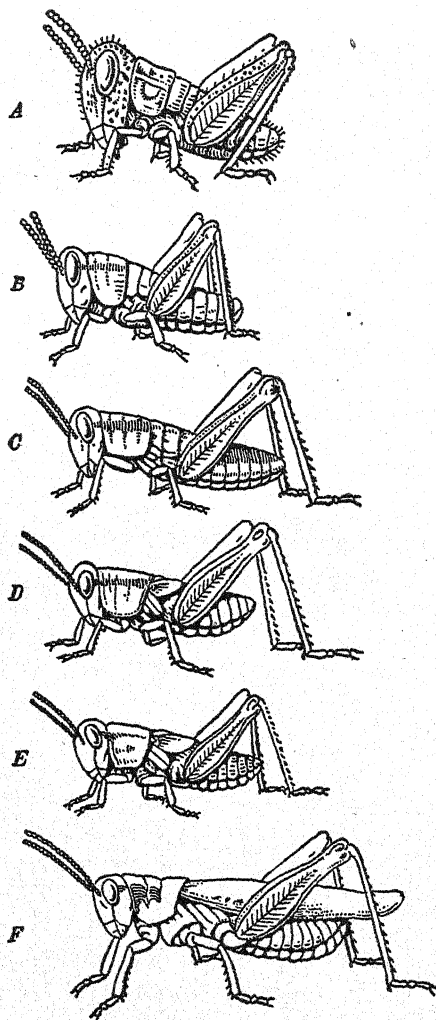


FIG. 371. Growth and differentiation of locust after hatching. *A* is recently hatched and more highly magnified than the other nymphs, which are shown after successive molts until the adult is seen at *F* (cf. Fig. 358). Note appearance of wing-pads in *D* and *E*.

(After A. S. Packard, from H. R. Linville and H. A. Kelly, "General zoölogy," copyright, 1906, by Ginn and Co., reprinted by permission.)

pair of wings into wingcovers, as in the Coleoptera and to a lesser extent in the Orthoptera and Hemiptera, and the reduction of the posterior pair of wings in Diptera are regarded as modifications of the more typical four-winged state. Since the development is direct and without metamorphosis in the simpler forms of insects, it is probable that the varying degrees of metamorphosis have been evolved from the direct type of development.

Order 1, *Thysanura* (tassel-tails). Common examples are the household pests known as fish-moths, silverfish, or slicks of the Genus *Lepisma* (Fig. 372 A). Mouthparts mandibulate. Development without metamorphosis. Species 250.

These may be regarded as the simplest of existing insects, because of primitive features such as the absence of wings in young and adult.

Order 2, *Collembola* (glue-pegs). Common representatives are the snow-flea, *Achorutes nivicola*, which appears on the snow in spring and is sometimes a pest to maple-sugar makers, and the spring-tail, *Podura aquatica*, frequently found on the surfaces of pools. Mouthparts mandibulate. Development without metamorphosis (Fig. 372 B). Species 1030.

Order 3, *Ephemera* (living but a day). The may-flies. Mouthparts mandibulate in nymphs but degenerate in adults. Wings membranous, posterior pair smaller and absent in a few species. Development with incomplete metamorphosis. The eggs of may-flies are laid on water, where the development occurs. The nymphs can be recognized by the three long caudal appendages and the gills upon the abdomen (Fig. 373). After many molts and at least a full year of this larval existence, the insect comes to the surface, casts its skeleton, and emerges as the fully formed adult. The adult lives but a few hours or at most a

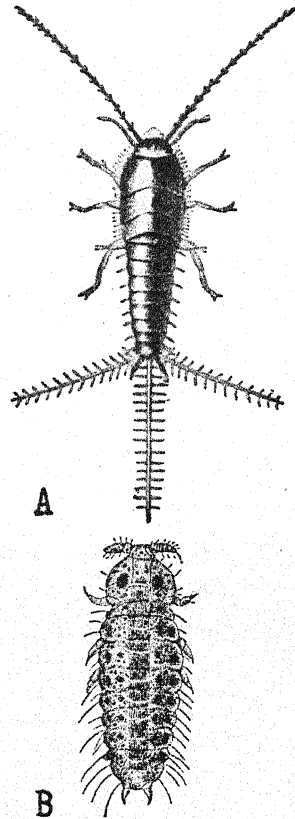


FIG. 372. Wingless insects. A, The silverfish, *Lepisma saccharina*, one of the Order Thysanura. B, the snow-flea, *Achorutes armatum*, one of the Order Collembola.

(A, from C. L. Marlatt, 1915, Farmers' Bulletin, No. 681; B, *op. cit.*, No. 789, U. S. Dept. Agriculture.)

THE ARTHROPODA

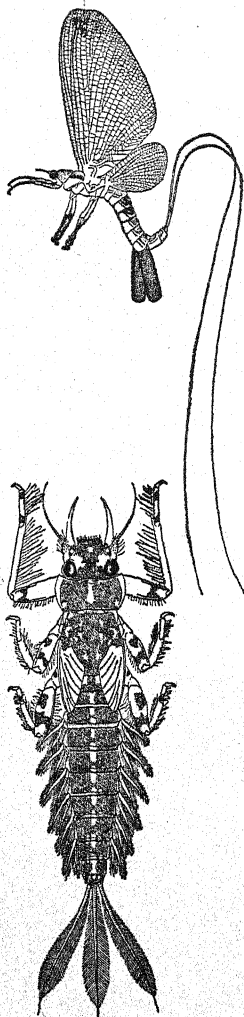


FIG. 373. The may-fly, *Polymitarcys albus*, one of the Order Ephemera. Above, the female hovering, with egg-packets extruding. Below, larval stage, on a larger scale.

(From J. G. Needham, 1917-18, Bulletin U. S. Bureau Fisheries, vol. 36.)

few days, during which sexual union occurs and the eggs are laid upon the water. Species 450.

Order 4, *Odonata* (toothed). The dragon-flies and damsel-flies. Mouthparts mandibulate. Wings, two pairs, membranous. Development, with incomplete metamorphosis, occurring in water. Species 2650.

Adult *dragon-flies* are wonderfully efficient in their powers of flight as they skim the surfaces of ponds in the heat of the day. Although they are often supposed to be dangerous, they are in fact beneficial to man, since they destroy innumerable small flies and mosquitoes which they catch in full flight. The name "mosquito-hawks," which is sometimes applied to these insects, is more appropriate than the other common names, "snake-doctors" and "devil's darning needles." The clumsy nymphs of dragon-flies are found crawling upon the bottoms of ponds and streams. Before the final molt they climb along the stem of a plant into the air, and after the adult emerges the cast skin of the nymph remains clinging to this support.

The damsel-flies, which are classified with the dragon-flies, are smaller and more delicate of body and wing.

Order 5, *Plecoptera* (folded-wings). The stone-flies. Mouthparts mandibulate. Wings, two pairs, membranous. Development, with incomplete metamorphosis, occurring in water. Species 480.

The nymphs of *stone-flies* somewhat resemble those of may-flies; they are commonly found in streams, attached to the under sides of stones. The adult life is of much longer duration than that of may-flies.

Order 6, *Orthoptera* (straight-wings). The locusts and related forms, such as the grasshoppers, katydids, crickets, cockroaches, and walking-sticks. Mouthparts mandibulate.

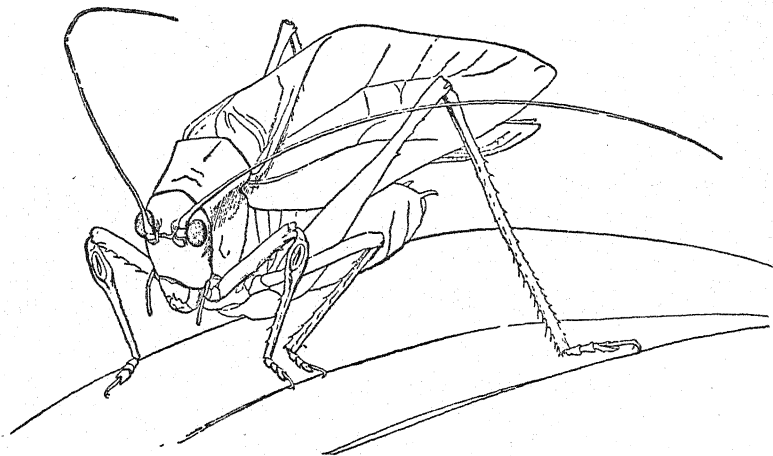


FIG. 374. The katydid, *Microcentrum rhombifolium*, one of the Order Orthoptera. Openings of the auditory organs are seen on second segment of each anterior thoracic appendage (cf. Fig. 368).

(From a sketch by B. Horsfall, 1925, *Natural History*, vol. 25, courtesy American Museum of Natural History and E. Dahlgren.)

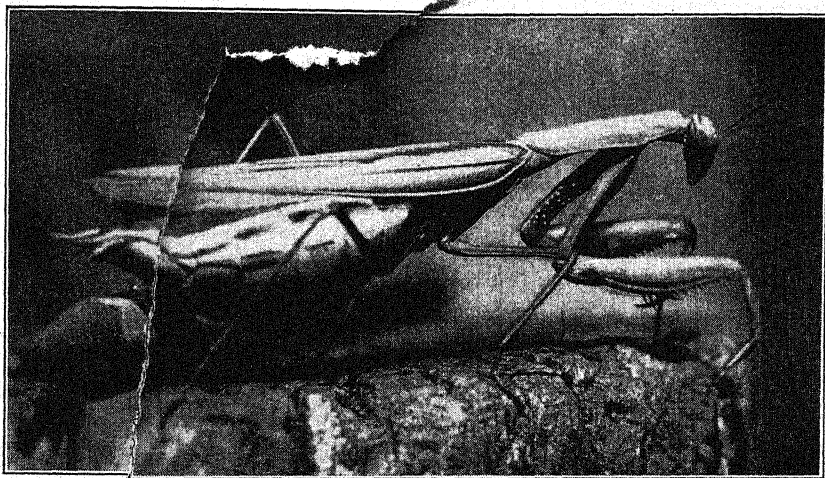


FIG. 375. The praying mantis, *Mantis religiosa*, one of the Order Orthoptera, is so called because of the attitude it assumes as it waits to seize its victims. It would be as well named if called the preying mantis.

(Photograph from Ward's Natural Science Bulletin, vol. 16. Courtesy of Ward's Natural Science Establishment, Inc., Rochester 8, N. Y.)

Wings with the anterior pair usually modified by thickening. Development with incomplete metamorphosis. Species 15,000.

The *crickets* and *katydids* resemble the grasshoppers sufficiently in their general external features to be recognized at once as allied forms (Figs. 374 and 375). The crickets that are most familiar are the house and field crickets of the Genus *Gryllus*. The hind legs are elongated for jumping, as in the locust. In many species the wings are reduced in size, and some crickets are wingless. The antennæ, which are long and slender, are highly specialized as tactile organs in correlation with the nocturnal activities of these animals. In the males certain veins of the wings are modified for sound production (*cf.* Fig. 367). The mole-cricket is a type having its anterior legs adapted for burrowing, like those of a mole. The katydids are like green grasshoppers with very long antennæ. Their "Katy did, Katy did, she did, she didn't" is a familiar sound in the evenings of late summer.

Order 7, *Platyptera* or *Isoptera* (broad-wings or equal-wings). The termites, or "white ants," which are not true ants. Mouthparts mandibulate. Wings, if present, two pairs and membranous. Development with incomplete metamorphosis. Species 500.

The *termites* are nest-building insects that have long been known as pests in tropical regions because of their destruction of man's possessions. Termites of temperate zones, such as the United States, are rapidly assuming economic importance because of their consumption of the wood used in dwellings. These insects feed upon cellulose, a carbohydrate that most animals cannot utilize for food. Interestingly enough, the termites themselves do not digest the cellulose. They have numerous flagellate protozoans in their digestive tracts, and these digest the carbohydrate upon which both protozoans and termites are nourished. Such a relationship is known as *symbiosis*, since it is mutually beneficial (*cf.* p. 319). If the termites are freed of their protozoans, they continue to eat cellulose but starve to death. One group of the termites has almost no protozoans in the digestive tract. These termites cultivate fungi which live upon dead wood, in the so-called "gardens" that are maintained within the nests. The termites can thus feed upon the wood that has been partially digested by fungi. Termites cannot stand exposure to dry air. Correlated with this idiosyncrasy is their construction of tunnels, in the earth and in wood, in which they travel when outside the nest. Thus, they are rarely seen and may produce considerable destruction before their presence is known.

Social organization in the termites is highly developed, with division of the labor among individuals of the colonies, which differ in struc-

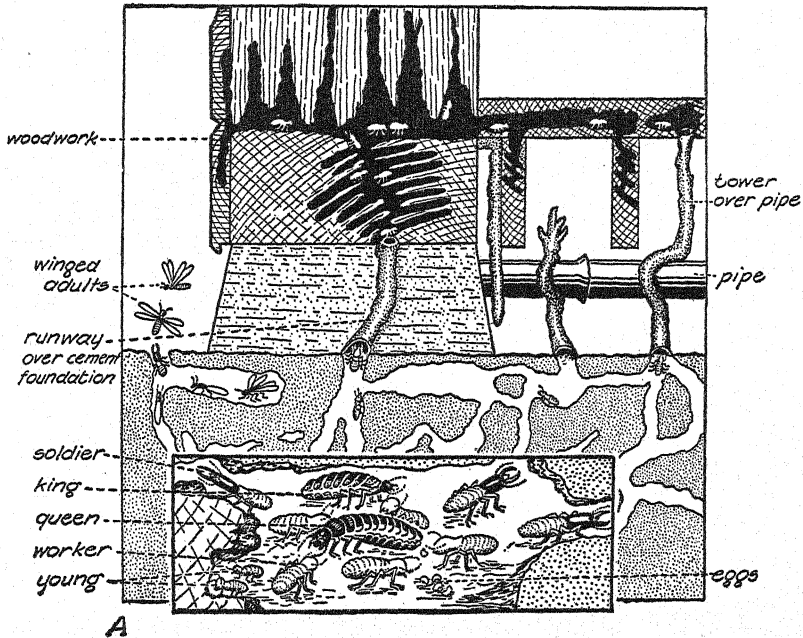


FIG. 376. Termites, Order Platyptera. A, the nest of a subterranean termite, *Reticulitermes hesperus*; diagrammatic. B, castes of *Termes lucifugus*. a, worker; b, soldier; c, perfect winged insect; d, insect after shedding wings; e, young, non-functional queen; f, older, non-functional queen.

(A, redrawn from S. F. Light, 1929, University of California Agr. Exp. Station Circular, No. 314; B, after B. Grassi and A. Sandias in J. W. Folsom, "Entomology," copyright 1906, by P. Blakiston's Son and Co., reprinted by permission.)

ture and constitute what are known as the *castes* (Fig. 376). The reproductive individuals, or *kings* and *queens*, are at first winged and soon after reaching maturity leave the nest in a flight of dispersion. A pair settle down together, break off their wings, and commence the excavation of a nest. After its completion mating occurs, and the queen begins to lay eggs. From these eggs are produced principally two kinds of individuals, *workers* and *soldiers*, both of which are infertile males and females. They are regarded as arrested nymphal stages that have undergone certain structural modifications. The workers, which are white, feed and clean the individuals of the other castes, as well as make additions to the nest and repair it. The soldiers, some of which have greatly enlarged mandibles, guard the king and queen and defend the nest against the attacks of intruders. The interrelations between the castes, the complicated feeding habits, the complex structure of the nest, and the associations with other organisms, both animals and plants, indicate the very high degree of specialization in this group (*cf.* p. 520).

Order 8, *Dermaptera* (skin-wings). The earwigs. Mouthparts mandibulate. Wings may be absent, or the anterior pair may form a wingcover for the membranous posterior pair. A prominent pair of pincers occurs at the posterior end of the abdomen. Development with incomplete metamorphosis. Species 740.

Order 9, *Thysanoptera* (tassel-wings). Thrips and related forms. Mouthparts suctorial. Wings present, rudimentary, or absent. Development with incomplete metamorphosis. Species 500.

Order 10, *Mallophaga* (hair-eaters). The bird-lice. Mouthparts mandibulate. Wings absent. Development with incomplete metamorphosis. Species 1350.

Order 11, *Anoplura* (unarmed-tail). The sucking or true lice. Mouthparts suctorial. Wings absent. Development with incomplete metamorphosis. Species 80.

Order 12, *Hemiptera* or *Heteroptera* (half-wings or different-wings). The true bugs, such as the cabbage-bug, the squash-bug, and the water-boatman. Mouthparts suctorial. Wings overlapping, the anterior pair thick at the bases and membranous at tips. Development with incomplete metamorphosis. Species 21,000.

The *squash-bug*, *Anasa tristis*, which is a pest upon squash and pumpkin vines the country over, is perhaps known best by its disagreeable odor (*cf.* Fig. 377). It is representative of true bugs with their sucking mouthparts and with wings showing the X-shaped pattern by which insects belonging to this order are commonly recognized. The adults hibernate over the winter, dying in the spring soon after the eggs

are laid upon the sprouts of the vines where the young are destined to feed. The nymphs hatch as wingless individuals and undergo a series of molts (Fig. 377 and cf. Fig. 371). They feed by piercing the leaves and stems of the plant with their beaklike mouthparts and sucking the juices.

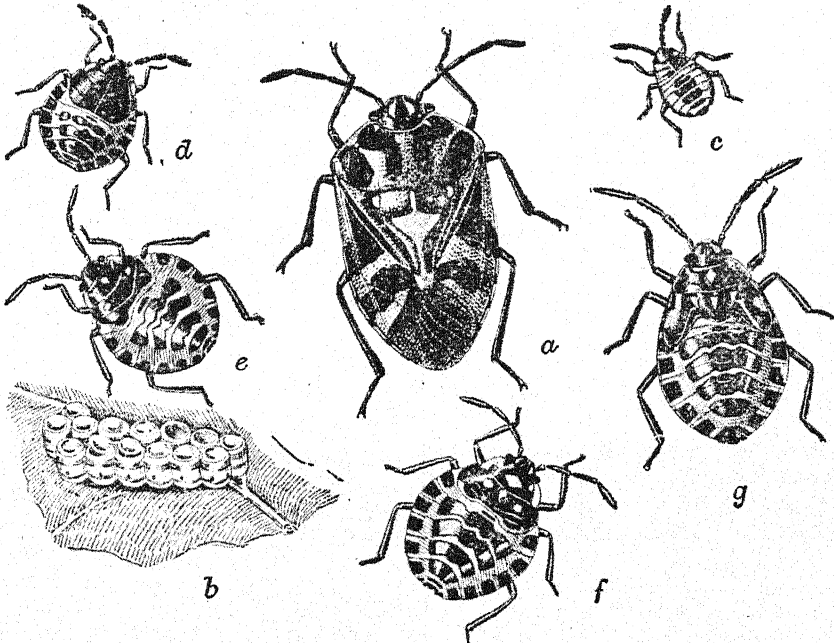


FIG. 377. The Harlequin cabbage bug, *Murgantia histrionica*, one of the Order Hemiptera, showing stages in its life-cycle. a, adult; b, egg-mass; c to g, nymphs.

(From F. H. Chittenden, 1920, Farmers' Bulletin, No. 1061, U. S. Dept. Agriculture.)

Order 13, *Homoptera* (like-wings). The cicadas, plant-lice, leaf-hoppers, and scale insects (Figs. 378 and 383 and cf. Fig. 518, p. 712). Mouthparts suctorial. Wings, when present, of the same thickness throughout and not overlapping. Development with incomplete metamorphosis. Species 16,000.

Order 14, *Coleoptera* (sheath-wings). The beetles (Fig. 379). Mouthparts mandibulate but forming a beak in weevils. The anterior pair of wings modified as covers beneath which the posterior wings are folded. Development with complete metamorphosis. Species 195,000.

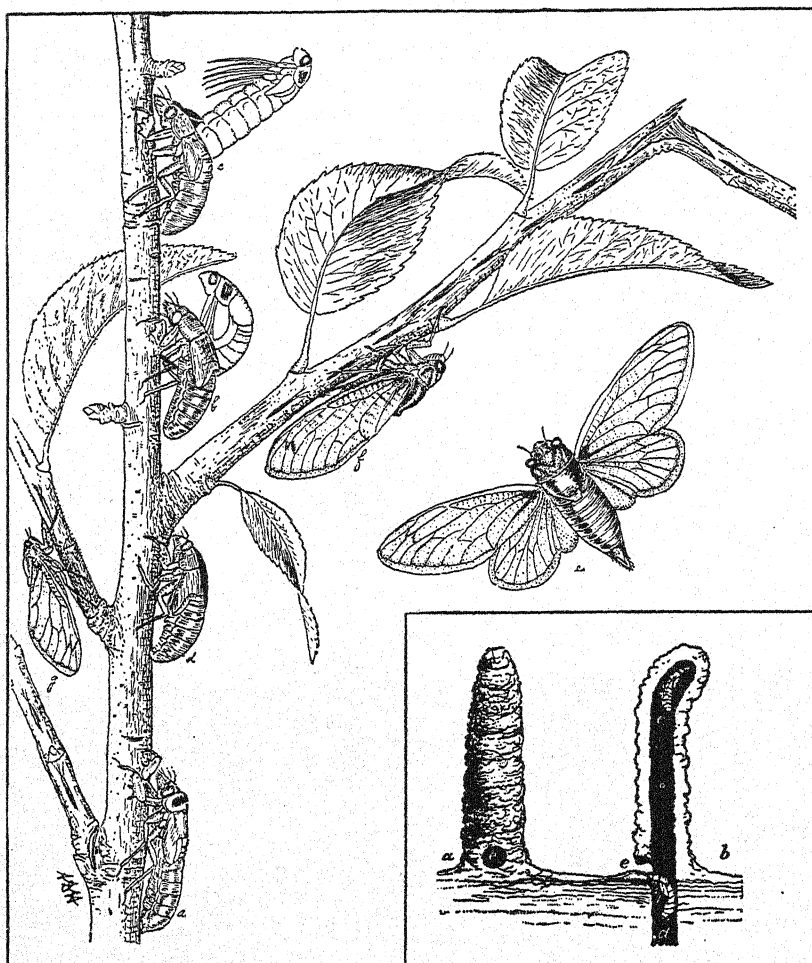


FIG. 378. The periodic cicada, *Tibicen septendecim*, one of the Order Homoptera. The eggs are laid under the bark of twigs, which is slit by the ovipositor of the female. After about six weeks the nymphs hatch and drop to the ground, into which they burrow. For seventeen years they live underground, feeding upon decaying material and juices from roots. Growth is very slow, and the nymphs probably molt only four to six times; they finally come to the surface of the ground and crawl up trees where the last molt occurs. *Below right*, galleries made by nymphs when they come to the surface: *a*, front view with opening at *e*; *b*, section showing nymphs at *c* and *d*.

* (Above, from W. E. Rumsey, 1935, Circular No. 70, West Virginia Agricultural Experiment Station. Below, from C. L. Marlatt, 1907, Bulletin No. 71, U. S. Bureau Entomology.)

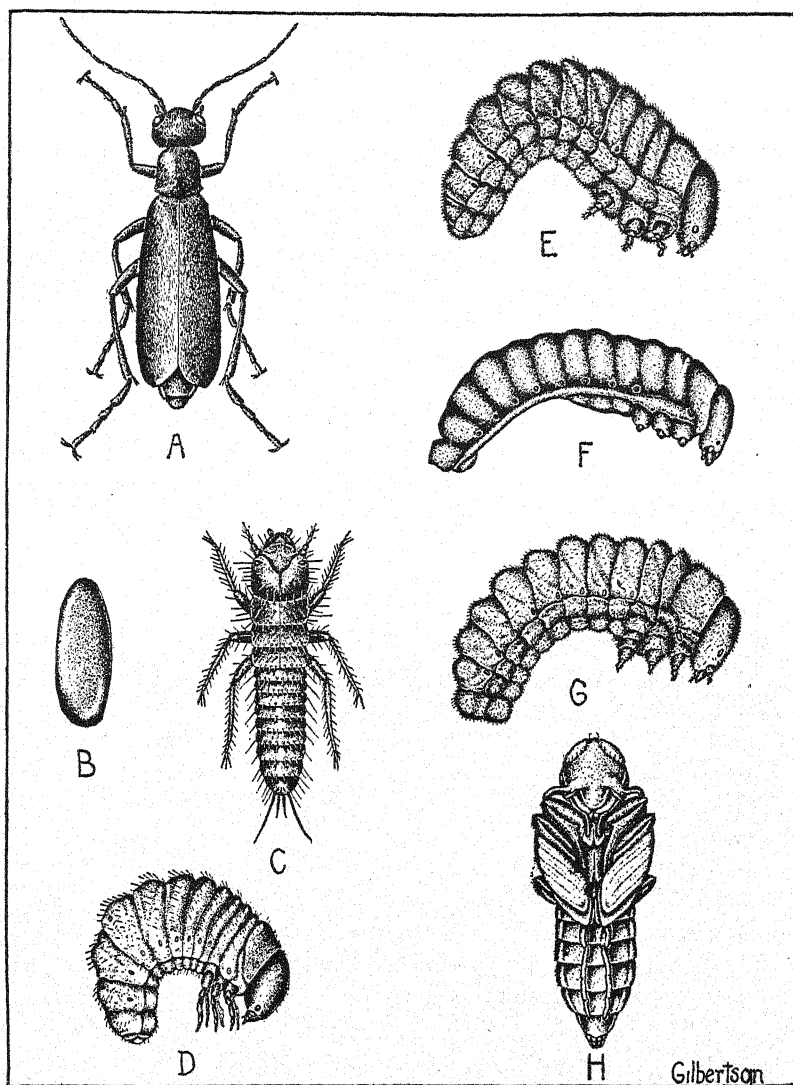


FIG. 379. Life-cycle of the immaculate blister beetle, *Macrobasis immaculata*. A, adult. B, egg. C, first larval stage. D and E, feeding stages of larva. F, wintering larva. G, last larval stage. H, pupa.

(From G. I. Gilbertson and W. R. Horsfall, 1940, Bulletin No. 340, South Dakota Agricultural Experiment Station.)

The Colorado *potato-beetle*, *Leptinotarsa decemlineata*, like other beetles, has the anterior pair of wings specialized into heavy wingcovers which meet on the median line and fit so tightly together that they seem upon first examination to constitute the dorsal side of a wingless body (cf. Fig. 379 and Fig. 518, p. 712). When, however, the wingcovers are pried apart, the functional wings are found folded beneath. The eggs are laid fastened to the leaves of the potato plant. The larvæ hatch as the humpbacked *grubs* that are so destructive to potato vines. When the larva has reached the end of its growth period, it crawls down the plant and burrows into the ground before undergoing the molt that produces the pupa. In a week or 10 days the adult emerges from the ground to continue feeding upon the potato plant. Taken as a group, the beetles, like the butterflies and moths, present a bewildering array of species adapted for many diverse conditions. Predaceous beetles haunt the ponds and streams in larval and adult stages; others bore into wood, particularly in their larval stages. The June-beetles winter in the ground as grubs and pupate in the spring to emerge as the adults that blunder against our lights in early summer.

Order 15, *Neuroptera* (nerve-wings). The ant-lion, the dobson-fly or hellgrammite, and related forms. Mouthparts mandibulate. Wings, two pairs, membranous. Development with complete metamorphosis. Species 2150.

Order 16, *Trichoptera* (hairy-wings). The caddis-flies. Mouthparts of adult rudimentary, mandibulate in larva. Wings membranous, hairy, posterior pair usually larger. Development with complete metamorphosis. Species 1600.

The larvae of *caddis-flies* construct tubes by fastening together bits of twigs, sand grains, shells, etc., with silken threads, which the larva spins. In locomotion the head and thoracic segments are extended, and the animal crawls along the bottom, dragging its tube. When disturbed, it withdraws and lies motionless. Before the larva transforms into the pupa, the tube is closed by a silken screen through which water can pass. When the adult emerges from the tube, it swims to the surface, climbs on some object above the water, and dries its wings before taking flight.

Order 17, *Lepidoptera* (scale-wings). The butterflies and moths. Mouthparts suctorial in adult but mandibulate in the larvæ, or *caterpillars*. Wings, two pairs, membranous and covered with scales. Development with complete metamorphosis. Species 92,000.

Among the *butterflies* the monarch or milkweed butterfly, *Anosia plexipus*, is one of our commonest species (Fig. 380 Above). It ranges

over all of North and South America and has begun the invasion of other lands, particularly western Europe, Australia, and the Pacific islands. The eggs are laid singly upon the leaves of various milk-weeds, and in a few days at summer temperature they hatch as minute larvæ. The larvæ feed voraciously and reach their full size in 2 or 3 weeks as caterpillars with light-green bodies conspicuously banded with black and yellow stripes and with pairs of antennalike filaments toward each end. The molt that closes this larval period produces the so-called *chrysalis*, or pupal stage, in which the distinctive adult features, such as wings and antennæ, are recognizable. After 10 or 15 days the individual molts for the last time and emerges as the adult. The wings are soft and crumpled at first, but they expand and stiffen within a short time as the butterfly clings to some object. In the fall the adults are either killed by the cold or migrate southward to pass the winter in subtropical regions and return to the north in the spring. Other butterflies have different seasonal relationships. For example, some spend the winter in the pupal state and others as eggs that hatch in early spring.

The *moths*, of which there are many species, are typically nocturnal in their activities, instead of typically diurnal like the butterflies, and fold their wings horizontally instead of vertically, as do most of the butterflies (Fig. 146 a, p. 227). They may also be recognized by the antennæ, which are fringed with many hairs and not enlarged at the ends like those of butterflies. Again, the pupal stage of a butterfly is typically a naked chrysalis attached to some object, whereas the pupæ of many moths are surrounded by *cocoons* of silk, which are spun during the last larval stage. When the pupal skin is molted within the cocoon, the adult moth forces its way out of the cocoon and, like the butterfly, is ready for flight after the expansion and drying of the wings. The household pest known as the clothes moth (Fig. 380 Below) is a familiar example of this order.

Order 18, *Mecoptera* (long-wings). The scorpion-flies. Mouthparts mandibulate. Wings, two pairs, membranous. Development with complete metamorphosis. Species 160.

Order 19, *Diptera* (two-wings). The true flies, such as the house-flies and mosquitoes. Mouthparts suctorial, although modified in various ways, as for lapping and piercing. The anterior pair of membranous wings functional, the posterior pair very rudimentary or absent. Development with complete metamorphosis. Species 51,000.

The common *house-fly*, *Musca domestica*, is perhaps the most familiar of all insects; and, since it has been recognized as a carrier of the germs of disease, its life-cycle is widely known (Fig. 381 Above).

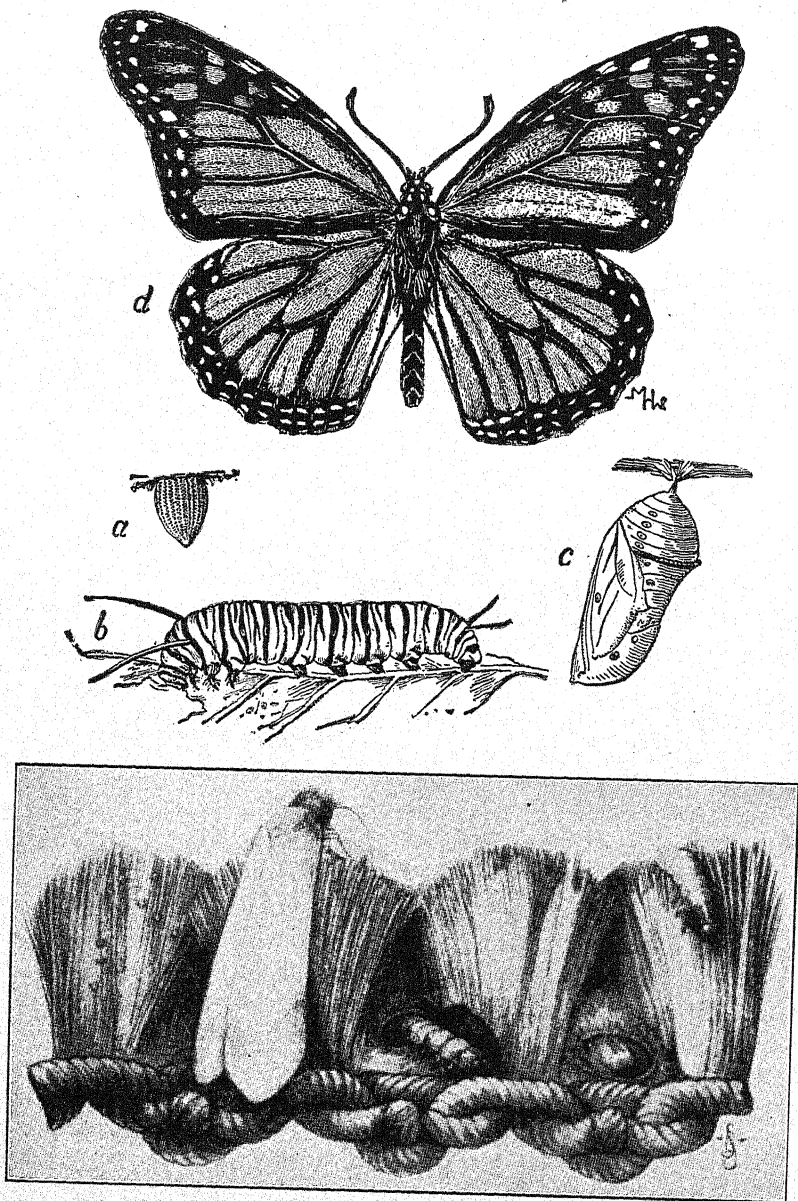


FIG. 380. Representatives of the Order Lepidoptera. Above, the monarch butterfly, *Anosia plexippus*: a, egg; b, larva or caterpillar; c, pupa or chrysalis; d, adult. Below, the webbing clothes moth, *Tineola biselliella*, attacking a carpet; viewed from edge of carpet, showing from left to right: eggs; adult moth; larva protruding from its tube; end of pupa in a cocoon; and larva crawling.

(Above, D. S. Jordan and V. C. Kellogg, "Evolution and animal life," copyright, 1907, by D. Appleton and Co., reprinted by permission. Below, from E. A. Back, 1940, Leaflet No. 145, Bureau of Entomology, U. S. Dept. of Agriculture.)

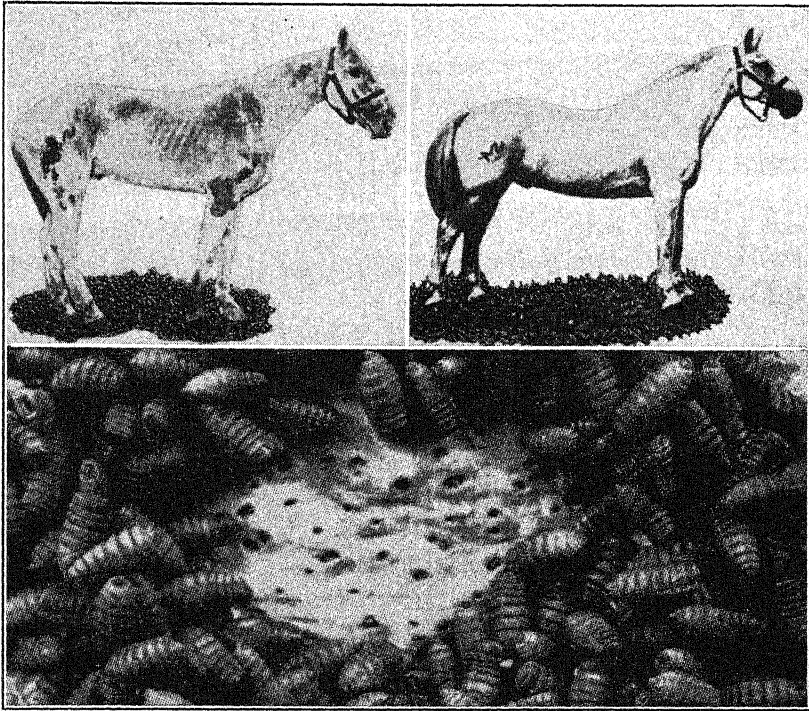
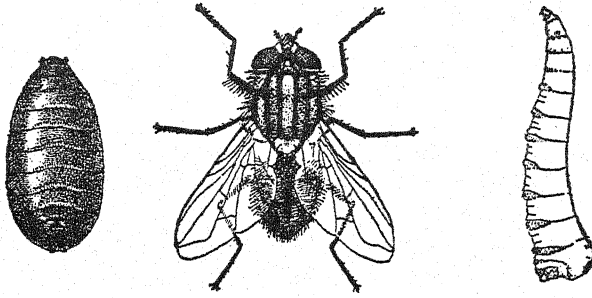


FIG. 381. Representatives of the Order Diptera. Above, the housefly, *Musca domestica*, showing adult (center), pupa (left), and larva or maggot (right). Below, horse parasitized by larvæ of the bot fly, *Gastrophilus*, before and after treatment with carbon disulphide; and the larvæ, or "bots," in horse's stomach.

(Above, from L. O. Howard, 1911, Farmers' Bulletin, No. 459, U. S. Dept. Agriculture. Below, courtesy of Extension Division, Michigan State College and of Illinois Agricultural Experiment Station.)

Like other Diptera, it has only the anterior pair of wings; the posterior pair are represented by the halteres or balancers, which are believed to function in maintaining equilibrium. Its mouthparts are adapted for biting and lapping, and the fly feeds upon almost any kind of organic matter that may be exposed. The extent to which house-flies may become distributors of bacteria can be shown by letting a single individual crawl across a sterile plate of gelatin and noting the colonies of bacteria that later appear along its trail. The eggs are laid in various forms of decomposing organic matter. The larvæ, or *maggots*, which hatch from these eggs in about 6 hours grow for 5 or 6 days before pupation, and the adult fly emerges in about 5 days. In this manner a generation may be developed every 12 days under favorable conditions; and, since each female lays about 100 eggs, the potential multiplication in a single season is great. Many of the individuals die with the coming of frosts, but some hibernate by crawling into protected places. They then emerge in early spring and lay the eggs from which the flies of another season arise.

Mosquitoes have assumed great importance since it was discovered about 1895 that certain species carry the malaria parasite and later that the virus causing yellow fever also is transmitted by mosquitoes (cf. p. 281). The adult females, in which the mouthparts are capable of piercing the skin and sucking the blood of man, are responsible for the transfer of these parasites, since the mouthparts of the male cannot pierce the human skin. Apparently the malaria parasite is restricted to mosquitoes of the Genus *Anopheles* and the virus of yellow fever to the Genus *Stegomyia* (*Aedes*). The most common genus of temperate latitudes is *Culex*, which does not serve as a host to either of these parasites. The species of the Genus *Culex* lay their eggs fastened together in little rafts that float upon the surface of the water (Fig. 382). The larvæ that hatch from these eggs are the *wrigglers* commonly seen in standing water, where they hang suspended from the surface film by tubes at the posterior ends of their bodies, through which air is admitted to their tracheal systems. The larval stage of *Culex* lasts from 1 to 4 weeks, according to the species and to some extent the temperature and food supply. The food during this period consists of minute organisms that are captured by the mandibulate mouthparts. With their third molt these larvæ change into active but non-feeding pupæ, in which the head and thoracic regions are enlarged and the wings and antennæ of the adult can be seen, as in the chrysalis of a butterfly. These pupæ must secure air from the surface as do the larvæ, but their air-tubes are located on the dorsal side of the thorax. After

2 to 5 days the pupal skin is cast, and the adult emerges. Both larvæ and pupæ are killed when the water is covered with oil, because they are dependent upon contact with the air for their oxygen. Another method of control is the elimination of stagnant water by draining swamps, as well as rainbarrels and empty cans.

Even before World War II mosquito control was becoming an international problem because of air traffic. Combatting the organisms of malaria, yellow fever, and other diseases borne by mosquitoes was

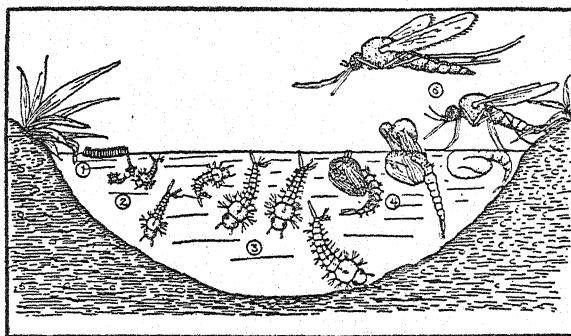


FIG. 382. The mosquito, *Culex*, one of the Order Diptera, showing stages in life-cycle. 1, eggs; 2 and 3, larval stages; 4, pupa; 5, emergence of adult from pupal skin.

(From T. J. Headlee, 1921, Bulletin No. 348, New Jersey Agricultural Experiment Station.)

becoming more difficult. The techniques of this control have been improved under the necessities of war. Increasing travel by air, however, will result in more danger from the transfer of the mosquitoes and of the human hosts that may harbor parasites dangerous to man.

Order 20, *Siphonaptera* (sucking, without-wings). The fleas. Mouthparts suctorial in adults, mandibulate in larvæ. Wings absent or rudimentary. Development with complete metamorphosis. Species 350.

Order 21, *Hymenoptera* (membrane-wings). The ants, bees, wasps, etc. Mouthparts mandibulate, often modified in the adults to form tongues adapted for lapping liquids. Wings membranous, either two pairs or absent. Development with complete metamorphosis. Species 67,500.

The Hymenoptera present an array of types, ranging from those of relatively simple habits to species with highly developed social organizations, such as honeybees and some ants. The examples that follow illustrate this diversity. The *gall-flies* are familiar because of their effect upon vegetation, although the adults are not popularly known.

The abnormalities produced in plants by the larvæ of these insects are illustrated by the oak-apples, or galls of oak trees. Dead oak leaves are often found on the tree or ground, showing the opening from which the adult gall-fly has escaped. The *ichneumon-flies* usually lay their eggs on the bodies of other insects (Fig. 383). After the larva hatches, it burrows within the body of the host and lives as a parasite until its time of pupation, when it comes to the surface and spins a cocoon from which the adult fly emerges. Caterpillars are sometimes found covered with the minute cocoons of these parasites. The parasitic

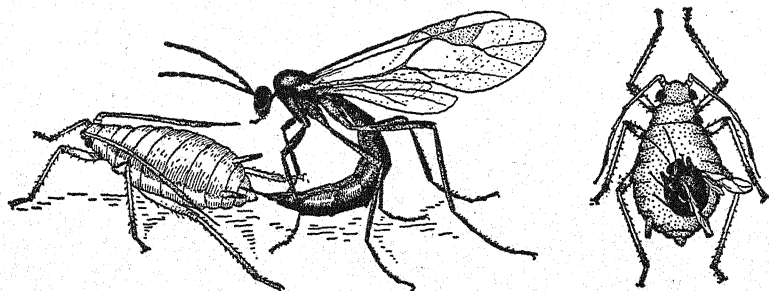


FIG. 383. A study in ecology. *Left*, an ichneumon-fly, one of the Order Hymenoptera, laying its egg upon an aphid, Order Homoptera. *Right*, emergence of the adult parasite after completing its development within the aphid.

(After Webster, from Circular No. 107, New Jersey Agricultural Experiment Station.)

species of the Hymenoptera far outnumber the better-known forms, such as the ants, bees, and wasps.

The *wasps* may be subdivided into the solitary wasps, in which there is no colonial organization, and the social wasps, which live in colonies like those of bees and ants. Mud-daubers of the Genus *Sceliphron* are solitary wasps that build a mud nest consisting of several tubes. When one of these tubes is completed, the wasp collects small spiders, which she paralyzes with her sting and with which she fills the tube, laying a single egg in the outer end before sealing. When the larva hatches, it utilizes the spiders as food and after pupation gnaws its way out as an adult insect. Only the females are active in this nest-building operation; the males apparently die soon after the mating. The digger wasps that excavate burrows, which they provision with insects, and those that excavate tunnels in the pithy stems of plants present further examples of such hunting and provisioning habits (Fig. 384). Among social wasps the species of *Polistes* represent a simple type of social organization (Fig. 385). They build nests of paper, obtained by the reduction of woody material to a pulpy mass somewhat after the man-

ner of human paper-making, although the mouthparts are the wasp's paper mill. A female, after hibernating through the winter, begins to construct a nest, which by the end of the season may reach a diameter of 20 or 30 centimeters. The single female, or *queen*, which begins this construction is soon aided in tending the young and adding to the nest by other females, the infertile *workers*, which hatch from her eggs.

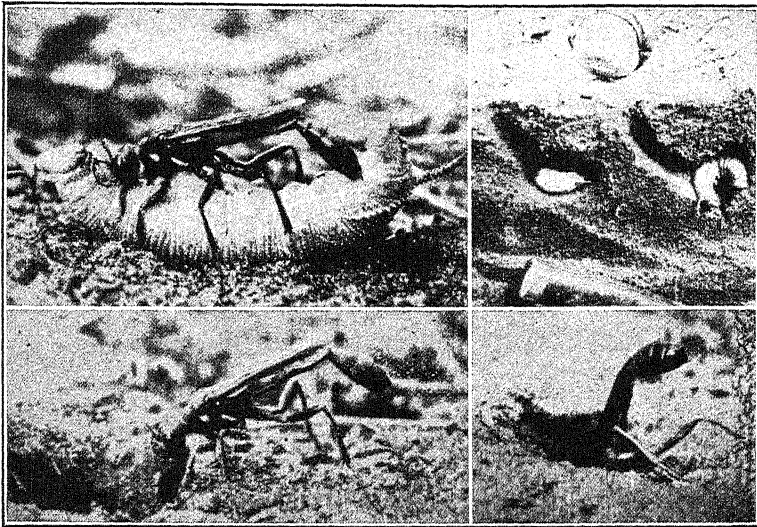


FIG. 384. The solitary wasp, *Ammophila*, one of the Order Hymenoptera, provisioning its burrow. *Left-above*, dragging to the burrow a caterpillar that it has paralyzed. *Right-above*, burrows containing same species of caterpillar shown on a smaller scale. *Below*, excavation of the burrow.

(From C. Hartman, 1905, Bulletin No. 65, University of Texas.)

The males are the *drones*, which do not work and die soon after mating. The nests of hornets that hang from the limbs of trees are composed of a series of combs resembling those of *Polistes* but enclosed in a common covering.

Among the *bees* there are solitary and social species and others that present transitional stages. Hence, it is possible to imagine the steps by which the highly organized honeybee colony may have evolved. In the solitary species each female constructs her own separate nest, in which an egg is laid and in which food is either stored or is brought to the larva during its development. Some of these solitary species, however, show a tendency toward gregariousness that suggests the beginnings of social life. They build many nests close together, although each nest belongs to a single individual. In others

the nests are separate, but the neighbors coöperate in the construction of a common entrance. The *bumblebees* represent a more specialized organization in which the females have become differentiated as fertile queens and infertile workers, and the males as drones, as is almost invariably the situation in social insects. A colony of *honeybees*, with its combs filled with stored food in the form of honey collected by the workers, with the single fertile female, or queen, which lays eggs and is tended by the workers, and with many drones, may be regarded as

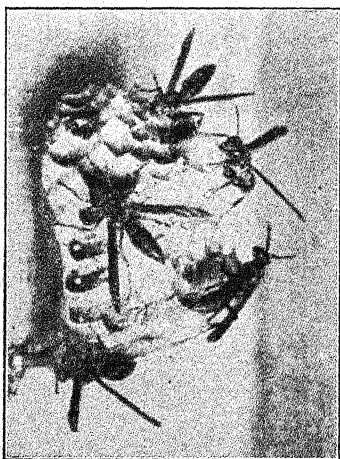


FIG. 385. The social wasp, *Polistes bellicosus*, one of the Order Hymenoptera, and nest.

(From C. Hartman, 1905, Bulletin No. 65, University of Texas.)

a further development of such a colonial organization as that of the *bumblebees* (Figs. 386 and 387). The specialized structures and habits of the workers and of the queen in a *honeybee* colony are remarkable. Food is collected and stored, the young are tended and fed, and the integrity of the colony with its single queen is maintained by the killing of additional queens or by the swarming of many workers with the old queen to found a new colony, leaving part of the old colony to rear a new queen. The behavior of the individuals is a marvel of precision and seeming adaptation of means to ends, although it consists of reactions based upon inherited reflexes that are modifiable only within the narrowest limits. How the characteristics of the workers can have arisen and been inherited, since the

workers leave no descendants, and the parthenogenetic origin of the males, which arise from eggs not fertilized at the time of laying and are, therefore, haploid individuals (*cf.* p. 116), are problems of considerable interest.

The *ants* are even more specialized in their social life, since there are no existing examples of solitary ants and since the workers of most ant colonies are specialized into two or more castes, which carry on special activities (Fig. 388). Ant colonies, particularly in some of the tropical species, may be very large, both in size of the nest and in number of individuals. The essential features of the social organizations are illustrated by many of our native forms. In a typical example, the males, which are winged throughout their brief existence, participate in the mating flight with the females and then die. These

queens then pull off their wings, establish nests, lay eggs, and tend the young until workers that can carry on these labors develop. When the mating season approaches, winged males and females are produced

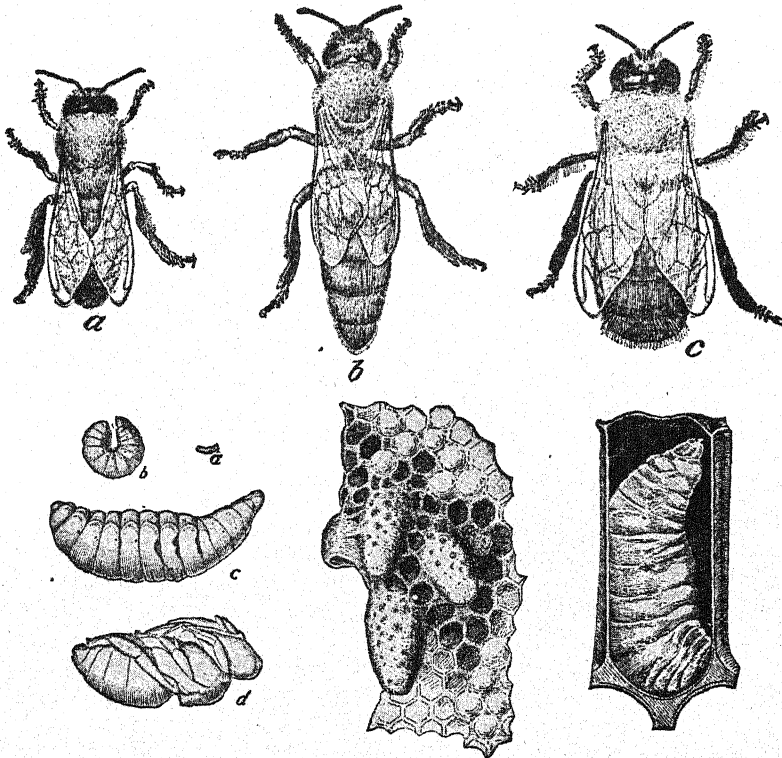


FIG. 386. Life-cycle of the honey-bee, *Apis mellifica*, one of the Order Hymenoptera. Above, a, worker, or sexually immature female; b, queen, or sexually mature female; c, drone, or male. Below-left, egg (a), larval stages (b and c), and pupa (d); center, comb showing some larger queen cells; right, side view of late larval stage within a cell.

(Lower right-hand figure from G. F. White, 1920, U. S. Dept. Agriculture, Bulletin No. 810; other figures from E. F. Phillips, 1911, Farmers' Bulletin, No. 447, U. S. Dept. Agriculture.)

and leave the nests in the swarms that are seen at certain seasons of the year.

The ants, bees, and wasps among the Hymenoptera and the termites (Platyptera) are of particular interest among the insects because of their social life and their behavior. From the standpoint of social organization the insects represent the only group in which

anything approaching the complexity of human society exists. From the standpoint of animal behavior, these insects exhibit amazing instinctive reactions, which are the result of inherited reflexes so fixed in their nature that they are hardly modifiable. Individuality and modifiability of nervous responses are perhaps better represented by

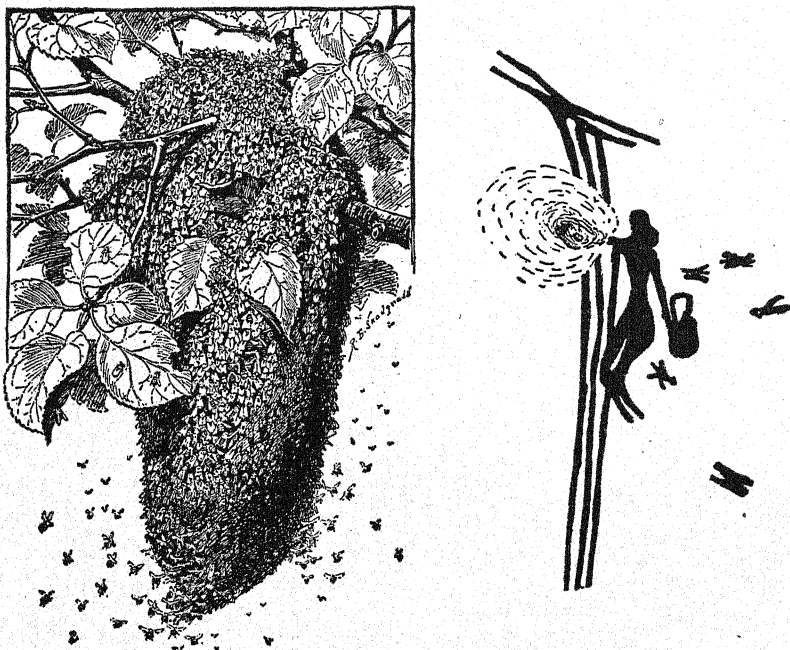


FIG. 387. Honey-bees. *Left*, a swarm of bees clustered on a branch. *Right*, pictograph believed to represent the collecting of wild honey in ancient times.

(*Left*, from *Farmers' Bulletin*, No. 1198, U. S. Dept. Agriculture. *Right*, from a prehistoric rock painting, Valencia, Spain; after Obermaier, courtesy of the Hispanic Society of America.)

forms such as the solitary wasps and the ichneumon-flies, although the individuality that has been claimed for the activities of these insects is probably exaggerated.

Importance of Insects to Man. Although a few insects, such as the silkworm and the honeybee, are specifically useful, a vast array of insect species are detrimental to man. Again, some insects have important rôles in the economy of nature, in the pollination of flowers, as food for many animals, or as destroyers of other insects that are harmful to crops. More often, however, the insect is destructive of the plant and animal life that is most necessary to man. Estimates made

for the United States in recent years place the total insect damage to crops, domestic animals, and stored products well in excess of a billion dollars annually. In the past man had to reckon more with his fellow mammals. In the present and for the future the insects, above all other animals, contend with him for the control of his environment.

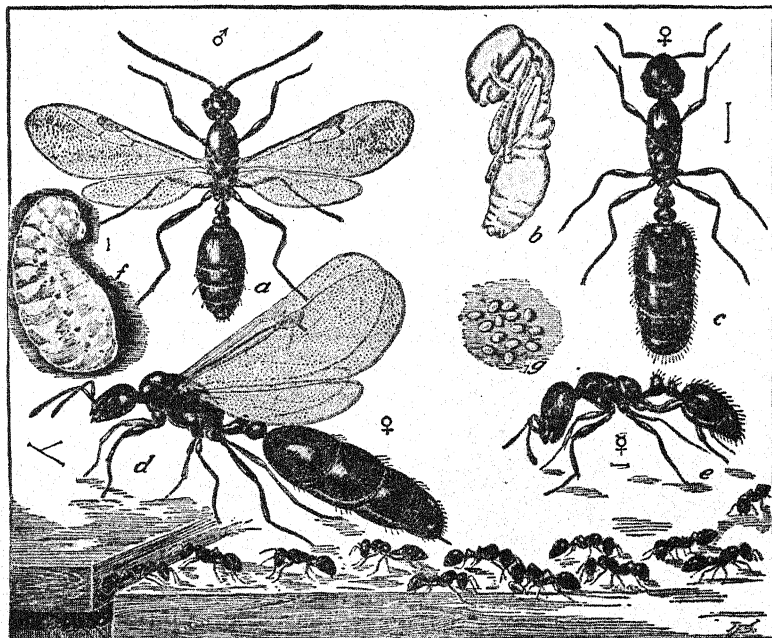


FIG. 388. The little black ant, *Monomorium minimum*, one of the Order Hymenoptera. *a*, male; *b*, pupa; *c*, wingless female; *d*, winged female; *e*, worker, or sexually immature female; *f*, larva; *g*, eggs; group of workers in line of march below.

(From C. L. Marlatt, 1916, Farmers' Bulletin, No. 740, U. S. Dept. Agriculture.)

Finally, many insects are dangerous to man as pests of his body and his habitations and, most important of all, as harborers of the germs of various human diseases.

Insects were a problem in ancient days as plagues upon man and beast as well as crops, but little could be done about them. With increasing scientific knowledge of insect activities and life-cycles and with intensification of the insect problem as a result of more intensive agriculture, man has devised many ways of combatting insect ravages. The science of entomology, or the study of insects, has assumed an increasing importance for this reason and now occupies a prominent

place in our agricultural colleges and experiment stations and in the United States Department of Agriculture. To deal with an insect problem, one must have all necessary knowledge regarding the particular species involved, its habitat, habits, and life-cycle. When these facts are known, methods of control may be devised and their effectiveness tested.

There are, of course, natural factors of insect control, such as temperature and humidity, soil conditions, parasites and other enemies,

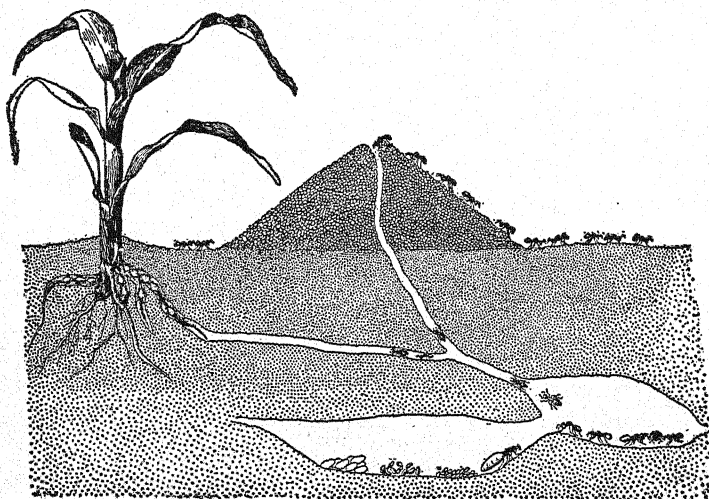


FIG. 389. A study in ecology: showing how ants foster the corn-root aphid. These aphids, which are cared for by the ants in their nests during the winter, are carried through tunnels to the corn plants and placed on the roots in the spring. Hence, anything that disturbs or destroys the ant colonies of a field reduces the number of aphids and promotes the growth of corn.

(From J. J. Davis, 1917, *Farmers' Bulletin*, No. 891, U. S. Dept. Agriculture.)

and diseases due to microorganisms. One year there may be a plague of locusts, apparently because the seasonal conditions were favorable to the development of more eggs; and the following year there may be relatively few locusts, apparently because the spring was cold and wet, or the parasites or disease germs more abundant. Man is concerned with a plague after its descent and, better yet, with its anticipation and control by preventive measures, as when fruit trees are sprayed in several different ways in the course of a season to insure a minimum of injury by insects. Thus, many techniques of insect control have been developed, and better ones are being sought.

To enumerate some of these controls, mechanical methods of hand-

picking and destroying the pests, cutting and destroying infested plants, digging deep furrows or erecting low fences of paper or sheet-metal, placing sticky bands on tree trunks, and the like, are sometimes easy and fairly effective methods. Another technique is cultural control, by pruning, fertilization, and other methods that result in vigorous growth and, therefore, in the production of plants better able to stand the attacks of insect enemies. The so-called clean-culture technique, in which the farmer destroys weeds, brush, and decaying vegetation that may harbor insect pests during late fall and winter, is believed useful in some cases. Crop rotation, time and method of plowing and tillage, time of planting and harvesting, and selection of varieties resistant to particular diseases are sometimes effective. In the use of all these techniques it is obviously necessary to know the habitats, the habits, and the life-cycles involved.

Ecological factors are sometimes turned to account, as when a predaceous enemy or a parasite which is fatal to an insect pest is introduced and "encouraged" to deal with the situation. A famous case of this sort was the lady-beetle brought from Australia to combat the cottony cushion scale, which had spread to California and was endangering the citrus crops of that region (*cf.* Fig. 518, p. 712). The introduced beetles destroyed most of the scale insects and have since been maintained for use against these pests as needed in subsequent years. This technique of nature, as it may be called, has been tried in other cases with some success. It is difficult because such predators and parasites may not be easily found, if they exist, and it is dangerous because any predator or parasite introduced into a new environment may turn to other prey or hosts with disastrous results to human interests.

The most widespread technique of insect control is by means of chemicals. These are sometimes used to repel the insects or to attract them to poisoned food and into traps, but most commonly they are employed as *insecticides*, which poison the insect in a variety of ways. Arsenic, sulphur, and fluorine compounds are among the most common poisons now in use, along with a variety of soaps, oils, nicotine compounds, and an increasing number of synthetic products. Among these last is the DDT (dichloro-diphenyl-trichloroethane) made famous by its use in World War II. Many ingenious devices have been developed for the application of these insecticides to growing plants. One of the latest is the use of airplanes and autogiros to spray or dust on a large scale or to reach areas not easily accessible by other means.

Insecticides kill in a variety of ways, notably as poisons when eaten with food or as means of stopping the insects' respiration by clogging

their spiracles and tracheal systems. The names and uses of insecticides are legion. The poison DDT is highly effective with certain insects and apparently ineffective with many others. The way in which it kills is not yet fully known. Perhaps it acts principally upon the nervous system.

DDT seems the best of all insecticides for indoor use because it kills almost every species of insect that is a household pest. Sprayed on surfaces and dusted into clothing, it will kill flies, moths, bedbugs, and other insects for months afterward. Moreover, it does not seem harmful to man when used in this manner. Out of doors the use of DDT is fraught with danger to many useful insects and other animals. For example, in certain concentrations it has been shown to kill many species of insects that are useful to man in the course of destroying others that are pests. In one case an oil solution of DDT sprayed from an airplane at a concentration estimated at 5 pounds to the acre killed all the birds in the forest so treated for extermination of the gypsy-moth. In a near-by forest, where only 1 pound of DDT was used to the acre, no birds were killed, but the gypsy-moths were destroyed as effectively as in the 5-pound area. In other experiments surface-feeding fishes were well-nigh exterminated, and deep-feeding fishes were affected by loss of insect food. Attempts at outdoor mosquito control with DDT have killed many edible fishes, crabs, and other shore-dwelling forms. Because of these deadly effects the federal government is conducting extensive experiments to determine the ways in which DDT may be used out of doors with safety to man and to animals of all sorts that are useful to man in the economy of nature. Until the results of such experiments become known, DDT should not be used except for household purposes.

By and large, the insects receive less attention in courses in general zoölogy than they deserve, particularly at inland institutions. This situation is due, perhaps, to the interest in marine animals that assumed such proportions in American zoölogy a half century ago and is still apparent in the teaching of elementary courses. The development of entomology as a separate science is also a factor. The great majority of Americans have had and will have little contact with marine animals, but everyone has contacts with insects. The city-dweller knows them as pests in his home or on trips to the country, the man of the country knows them as pests not only of himself but of domesticated animals and crops as well. Insects that are carriers of disease are becoming better known, and such knowledge of particular species may be of life and death importance. In addition to these practical matters which interest the layman, the insects present the biologist and the nature

lover with a bewildering array of biological material. At one extreme is such an insect as the fruit-fly, *Drosophila*, which has been a boon to the students of heredity and is increasingly used for other technical research. At the other extreme are the innumerable insects that are objects of beauty and fascination to the amateur naturalist. With so many insects at hand, anyone with an interest in them may find a hobby or an avocation of life-long interest. Insects are, indeed, the greatest of all the invertebrate groups in number of species and in diversity of structure and habits, and such insects as the social and the solitary hymenoptera represent the highest level of intelligence among invertebrates, as do the higher mammals and man among vertebrate animals.

The Onychophora

The Genus *Peripatus*, which is distributed principally in the warmer parts of the southern hemisphere, is the only living representative of

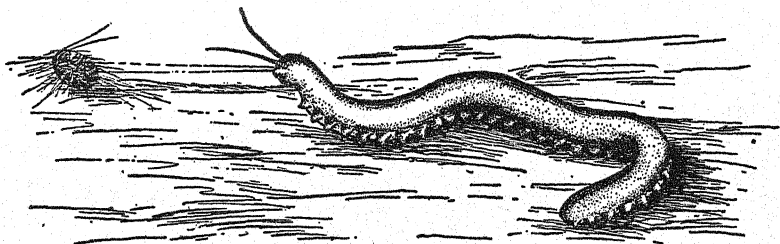


FIG. 390. *Peripatus*, entangling a cockroach in sticky threads discharged from two papillæ beneath the head.

(From A. S. Pearse, "General zoölogy," copyright, 1917, by Henry Holt and Co., reprinted by permission.)

the Onychophora (Fig. 390). These animals are wormlike, possess tracheæ, and live in moist places under bark or objects on the ground, in the same manner as the larvæ of many beetles. A general resemblance to an annelid worm, with its terminal mouth and anus and a pair of appendages on each segment of the body, is apparent. Certain features of their anatomy suggest the possible ancestry of the Class Insecta as well as a relationship between the whole arthropod phylum and the Annelida. They are sometimes classified as a separate phylum.

The Myriapoda

In this class of arthropods are included the centipedes, or hundred-legged worms, and the millipedes, or thousand-legged worms (Fig. 391).

These are familiar animals in all temperate and tropical countries, living in damp places under stones and timbers and in the upper layers of the soil. There is a head region, but the wormlike shape

of the body and the pair of appendages on each somite are primitive features. In the subdivision of the class that includes the millipedes there are two pairs of legs on each somite. Respiration is carried on by a tracheal system, as in the insects. When all the facts of their structure and development are considered, it seems that the Myriapoda are the Arthropoda most closely related to the Insecta.

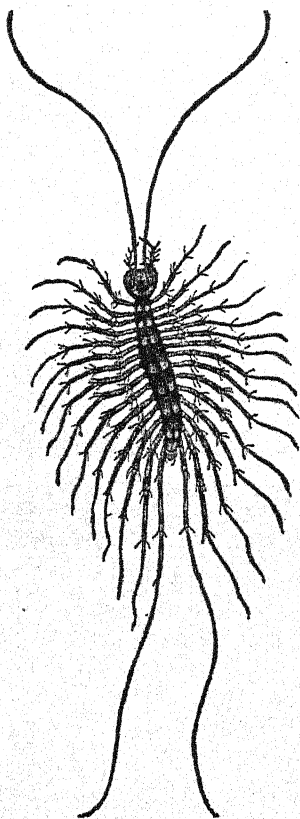


FIG. 391. The house centipede, *Scutigera forceps*.

(From C. L. Marlatt, 1914, Farmers' Bulletin, No. 627, U. S. Dept. Agriculture.)

The Arachnida

The most familiar examples are the many species of spiders, although scorpions, mites, and ticks of various sorts belong to this class (Figs. 392, 393, and 394). The arachnids are characterized by six pairs of jointed appendages, of which two pairs are mouthparts and four pairs are locomotor organs. The Genus *Limulus*, known as the horseshoe crab, is classified with the Arachnida, because it has these six pairs of appendages and certain other resemblances (Fig. 394). The horseshoe crabs, however, are marine and are of gigantic size as compared with other Arachnida. The relationship is remote, since *Limulus*, like the brachiopod *Lingula* and the cephalopod *Nautilus* (cf. pp. 405 and 436), is a genus that has persisted from a very early geologic period without important changes of structure.

Like the insects, the spiders (Fig. 392) are animals that have been unduly neglected by zoölogists, and for similar reasons (cf. p. 526). There is also a popular prejudice against them because they are "crawly" things and because of a few species, such as the black-widow spider, *Latrodectus mactans*, which have a poisonous bite. It is true that some of these poisonous species, taken the world over, are dangerous pests and that others may inflict painful bites. But many

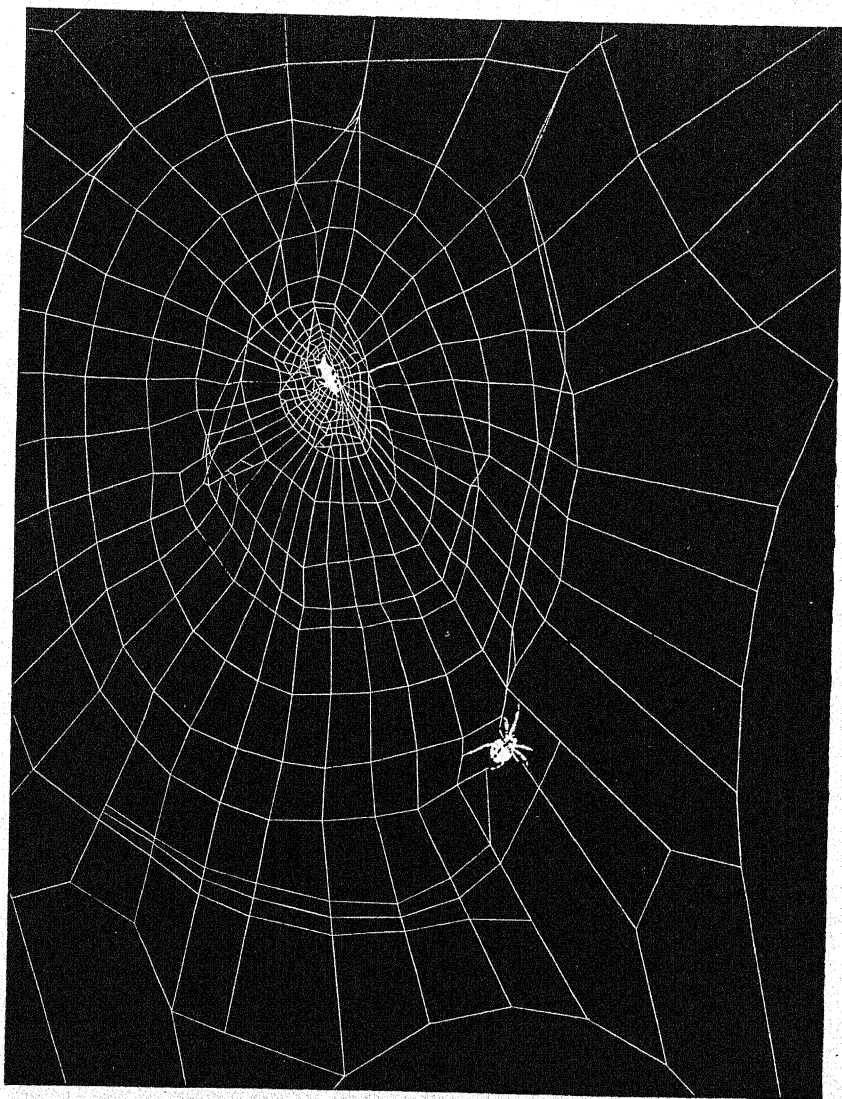


FIG. 392. Arachnida: Spider weaving adhesive threads into a partially constructed web (*Continued*, p. 530).

(Kodatron Speedlamp photograph by H. L. Gibson, A. P. S. Courtesy of Mr. Gibson and of Ward's Natural History Establishment Inc., Rochester 8, N. Y.)



FIG. 392. Arachnida: The spider, *Miranda aurantia*, and its web. Threads of this silk are used for the cross hairs in optical instruments (*Concluded*).

(Photograph by Ewing Galloway. From Cenco News Chats, May 1940. Courtesy of Mr. Galloway and of Central Scientific Company.)

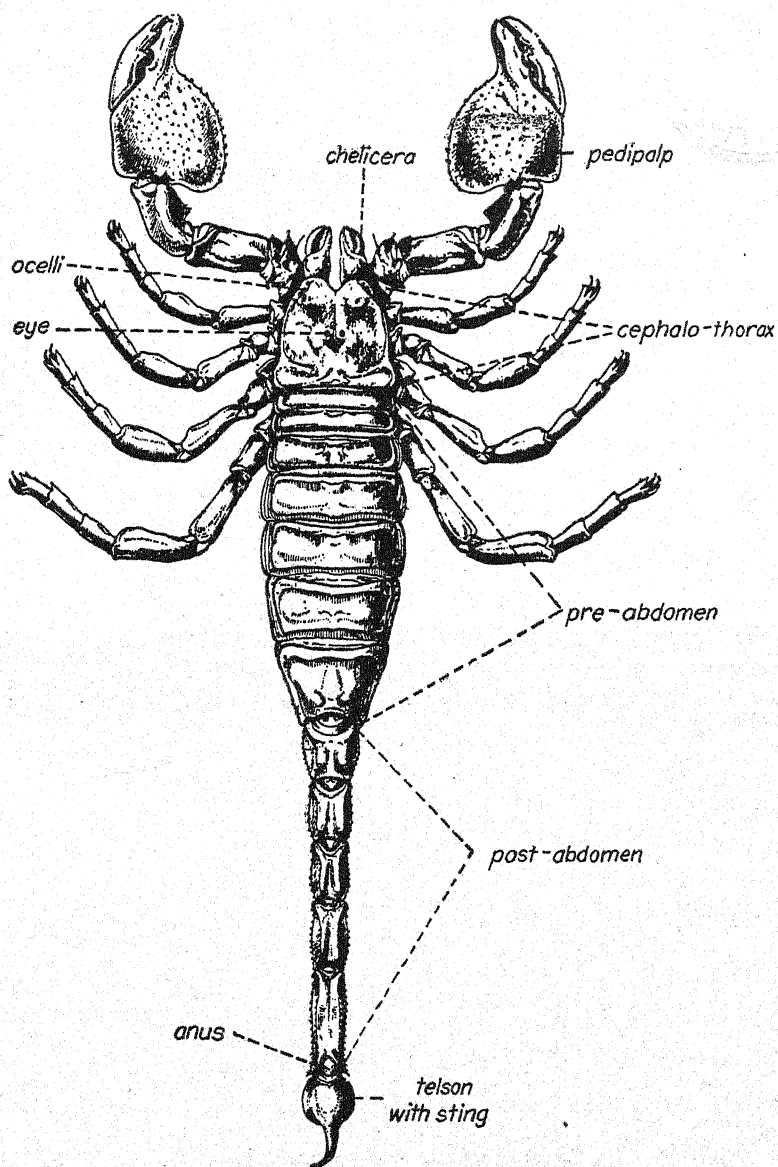


FIG. 393. Arachnida: A representative scorpion, *Pandinus imperator*, dorsal view.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

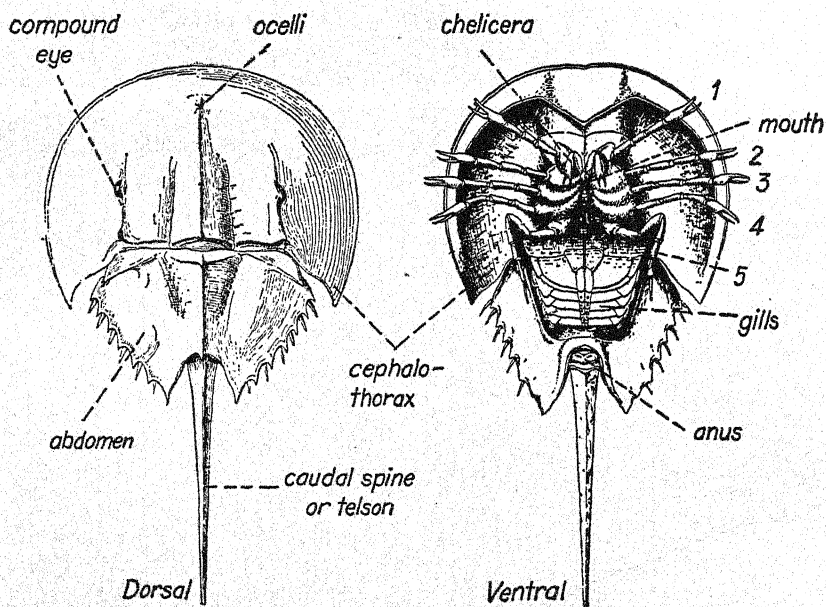
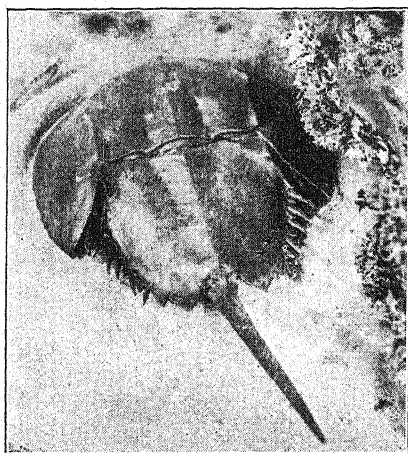


FIG. 394. Arachnida: The horseshoe crab, *Limulus polyphemus*, survivor of an ancient fauna and classified as an arachnid. Above, crawling upon the sand in shallow water. Below, external features.

(Above, from Roy W. Miner, 1925, *Natural History*, vol. 25. Courtesy of author and of American Museum of Natural History. Below, from W. Stempell, *op. cit.*)

more species are useful to man by their destruction of insect pests and are otherwise important in the economy of nature. The habits of spiders present fascinating material for the study of animal behavior at a high level for invertebrates. Many species are available close at hand for observation in nature. Many can be maintained in the laboratory or at home in simple cages that enable one to observe their interesting activities.

The Arthropod Body-plan

The schematic arthropod is an animal that is externally metameric in the same way as an annelid but has a pair of jointed appendages on each somite and is covered with an exoskeleton (Fig. 395). Internally, the arrangement of the digestive system and the nervous system resembles that of an annelid. On the other hand, there is no system of closed blood vessels and no body cavity resembling the coelom of the annelid. The rudimentary cavities at the inner ends of the excretory organs and perhaps the cavities within the reproductive glands may be the degenerate remnants of a coelom that was well developed in the ancestors of arthropods. The circulatory systems can be compared only in so far as both arthropods and annelids have pulsatile dorsal vessels which drive the blood anteriorly.

The excretory organs of the Crustacea are regarded as greatly modified nephridia. There are, in different crustaceans, two pairs of these organs, one, in Malacostraca, opening on the antennal somite, and another, in Entomostraca, opening on the somite bearing the second maxillæ. Hence, if this interpretation of the excretory organs is correct, two pairs of nephridia on two different somites are represented in the Crustacea. If the arthropods have descended from an annelid-like ancestor, it must be supposed that the pairs of nephridia once present in most of the somites have disappeared during the evolution of these animals. In the Insecta there are no organs that can be regarded as modified nephridia, and excretion is performed by organs peculiar to the insects, the Malpighian tubules. In the Onychophora, which are regarded as resembling the ancestors of insects, there are paired nephridia in most of the somites, as in annelids. Again, in the Myriapoda there are no signs of modified nephridia, but in the Arachnida the so-called coxal glands can be regarded as greatly modified nephridia. With respect to the shape of the body, the Myriapoda and Onychophora are more wormlike than the Crustacea and the adults of Insecta, and the metamerism is thus apparent externally from end to end of the body. The Insecta, the Arachnida, and such Crustacea

as the crayfish, lobsters, and crabs are the more specialized members of this great phylum.

In concluding the account of this phylum, which so abounds in species and individuals, the evolution of its members in relation to their environment may be noted. The evidence points to the ocean as

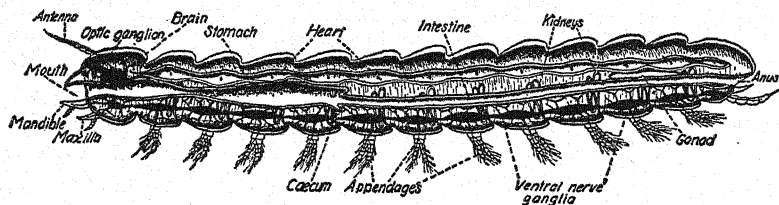


FIG. 395. Schematic arthropod; the parts labeled kidneys correspond to the nephridia of the earthworm.

(From A. S. Pearse, "General zoology," copyright, 1917, by Henry Holt and Co., reprinted by permission.)

the primitive habitat of the arthropods, as of other major groups of animals, and there are interesting parallels between the Arthropoda and the Chordata in the apparent evolution from aquatic to terrestrial life and in the return of certain forms to the water. The Crustacea, which in certain respects are the simplest of the arthropods, are primarily aquatic animals, but some members of this class, such as the sow-bugs, have become adapted for life on the land. Although the Insecta are as completely adapted for their terrestrial life as the mammals among vertebrates, many insects have returned to the water for a part or the whole of their life-cycles, as have the seals and whales among mammals.

CHAPTER 17

THE ECHINODERMATA

The Echinodermata are non-metameric, triploblastic, coelomate animals with a five-parted radial symmetry masking an underlying and primitive bilateral symmetry, with a calcareous endoskeleton of spicules or plates, with a unique set of vessels called the water-vascular, or ambulacral, system, and without nephridia. They are well named the "spiny-skinned" animals, because spines are present in so many species. The phylum is divided into the Subphyla *Pelmatozoa*, *Asterozoa*, and *Echinozoa*. The Pelmatozoa include the Class *Cystoidea* and the Class *Blastoidea*, which are extinct, and the Class *Crinoidea*, or sea-lilies, which are now represented by few species as compared with their abundance in earlier geologic times. The Asterozoa include the Class *Asteroidea*, or common starfishes, and the Class *Ophiuroidea*, or brittle-stars and basket-stars. The Echinozoa include the Class *Echinoidea*, or sea-urchins and sand-dollars, and the Class *Holothuroidea*, or sea-cucumbers.

Echinoderms are typically bottom-dwelling animals that move slowly if they are not permanently attached. They are exclusively marine, and there is no evidence from the fossil record that any members of the phylum have ever become established in fresh water, although a few tropical species can live in brackish water. At one time they were classed with the Cœlenterata because of their radial symmetry, but further study showed that the radial symmetry of echinoderms differs markedly from that of cœlenterates and that echinoderms are triploblastic animals with a coelom. A puzzling feature in the development is the formation of a bilateral larva, from which the radially symmetrical adult is derived by a complicated metamorphosis. These features of symmetry and development make the echinoderms very interesting animals. As one anatomist has remarked, "They are in all things strange." Although they can be defined in the general terms used for other phyla, their structure seems quite unlike that found in such phyla as the Mollusca, the Annelida, and the Chordata. More careful examination, however, reveals that the echinoderms are not so radically different as they seem. They appear to be animals with a

radial symmetry, which was imposed upon an original bilateral symmetry at an early stage of their evolution. When so interpreted, their structure becomes intelligible in comparison with that found in other phyla. Indeed, they seem more closely allied to the chordate stem than to any other large group of animals (*cf.* Fig. 150, p. 233), although this relationship is remote. From an economic standpoint they are unimportant, except for the depredations of starfishes, which sometimes destroy whole beds of clams, oysters, and salt-water mussels. One of the few echinoderms used as food by man is a sea-cucumber which is esteemed under the name of *bêche-de-mer*, or trepang. Neither do echinoderms serve as food for many other animals; their spiny surfaces and the fact that many species are so largely composed of skeleton have doubtless made them relatively free from destruction by predatory enemies. This chapter reviews these animals and compares their structure and activities with those of other phyla.

The Asteroidea

The Starfish: *General Structure and Activities.* The following account of a starfish applies particularly to *Asterias forbesi* of the Atlantic Coast (*cf.* Figs. 396 and 397). This species is found upon rocky and shelly bottoms, from high-tide mark to a depth of about 125 feet, where the mollusks that constitute the greater part of its food are most

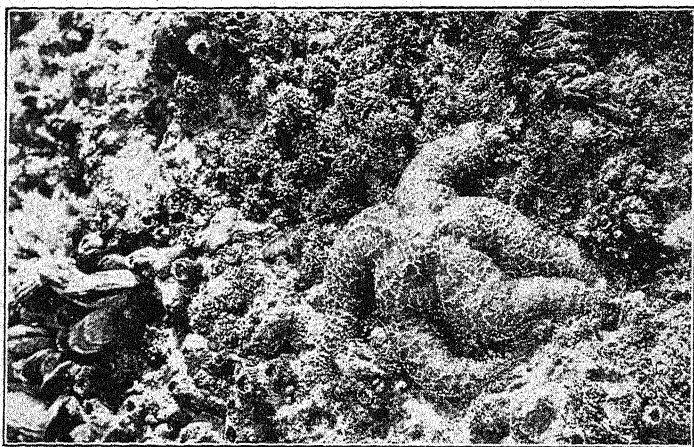


Fig. 396. A starfish in its natural habitat upon the bottom. Rock-barnacles and salt-water mussels are also shown.

(Photograph by courtesy of Pacific Biological Laboratories, Pacific Grove, California, and of George Stone.)

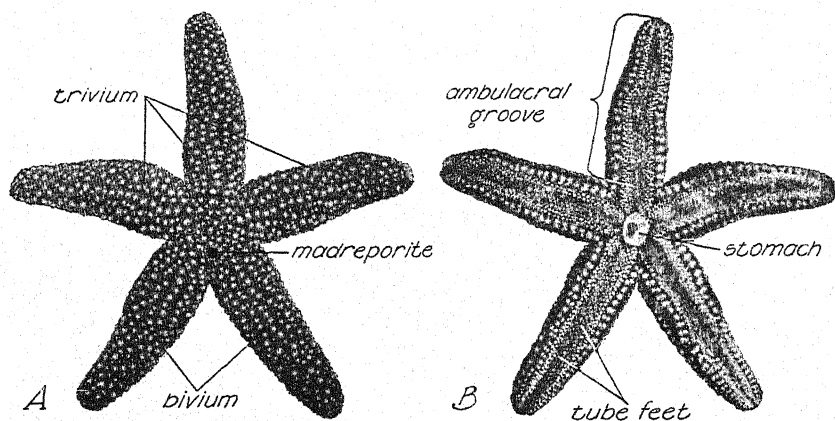


FIG. 397. A, the aboral surface of *Asterias forbesi*. B, oral surface of same; the stomach is everted and the tube feet are contracted.

(From W. R. Coe, 1912, Connecticut State Geological and Natural History Survey, Bulletin No. 19.)

abundant. It sometimes occurs on muddy and sandy bottoms and may crawl up the piles of wharves in search of food. Upon rocky shores it is often found in the pools left by the receding tide. The body consists of a *disk* and five radiating *arms*, each of which may be called a *radius* (Fig. 397 A). The upper or *aboral surface* is covered with *spines*, which are part of the skeleton (*cf.* Fig. 398). The surface between the spines bears projections called *papulae*, or *gills*, which function as respiratory and excretory organs. Around the bases of the

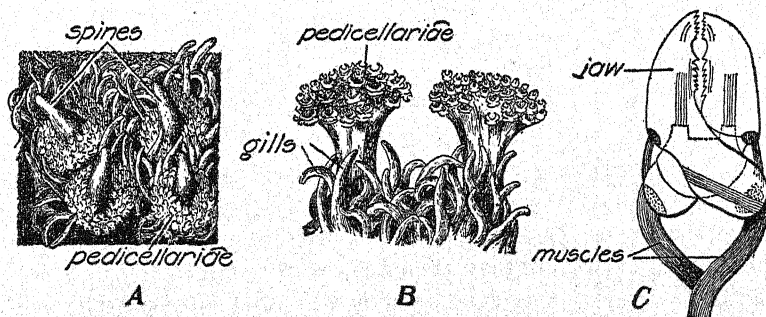


FIG. 398. Papulae and pedicellariæ of the starfish, *Asterias forreri*. A, portion of the external surface, showing spines, papulae or gills, and retracted rosettes of pedicellariæ. B, portion of the surface, showing rosettes of pedicellariæ extended so that they cover tips of spines. C, structure of a pedicellaria; diagrammatic.

(From H. S. Jennings, 1907, University of California Publications in Zoölogy, vol. 4.)

spines and among the papulæ are minute, pincerlike structures, the *pedicellariæ*, which function in keeping the surface free from foreign matter. At one side of the disk, between two of the arms, is a sievelike plate, the *madreporite*, by which the internal ambulacral system communicates with the outside. The two arms, one on each side of the madreporite, are called the *bivium*; the other three, the *trivium*

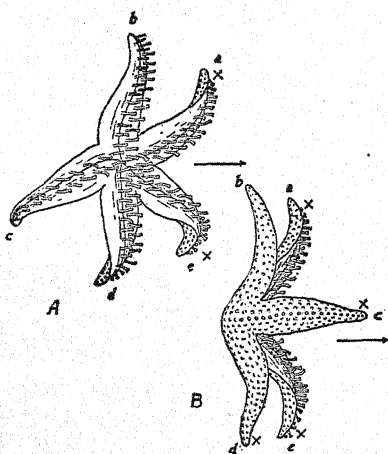


FIG. 399. Starfish righting itself. The arrow indicates the direction of turning; note that all the tube feet are extended in that direction. A and B are successive positions; a-e are comparable arms; and X indicates the arms that have tube feet attached to the substratum.

(After L. J. Cole, 1913, Jour. Experimental Zoölogy, vol. 14.)

(Fig. 397 A). The *mouth* is on the *oral surface* in the center of the disk surrounded by a membrane, the *peristome*; and radiating from this along the arms are the *ambulacral grooves* from which project the locomotor organs called *tube feet* (Fig. 397 B). At the end of each ambulacral groove is a small, reddish *eye-spot* below a short *tentacle*.

The starfish creeps slowly along the bottom by means of its tube feet. Although it seems inflexible and its arms may be broken off by rough handling, it can bend and twist in a great variety of ways. For example, when a starfish is turned upside down, it rights itself by twisting the arms until some of the tube feet become attached to the substratum and the animal can turn itself back to the normal position (Fig. 399). All this locomotion is effected primarily by the tube

feet, which terminate in suckers that can adhere firmly. These suckers seem to be useful on occasion, as when a starfish walks up the glass side of an aquarium or reaches out as though seeking another surface on which it might crawl; but they are not necessary for locomotion, because the animal can move over sand or upon a greased surface. The mechanism by which tube feet operate is explained in connection with the ambulacral system, of which they are a part (*cf.* p. 545). There is nothing like a head or an end that goes foremost. The starfish can travel in any direction in the plane of its rays, but, once started in a particular direction, the arms and tube feet behave in a coordinated manner that moves the animal steadily along until it encounters some-

thing to change the course of locomotion. A similar coördination is seen in the righting reaction when all the arms and their tube feet move in coördination as soon as a firm hold has been secured by some of the feet on one of the arms.

Structures and Functions Related to Metabolism and Irritability. The food of the starfish consists principally of mollusks, such as clams, oysters, scallops, and snails. In feeding, the arms are wrapped about the prey, and the tube feet are attached to the outer surface of the bivalve shell, which is eventually opened (Fig. 400). How this opening

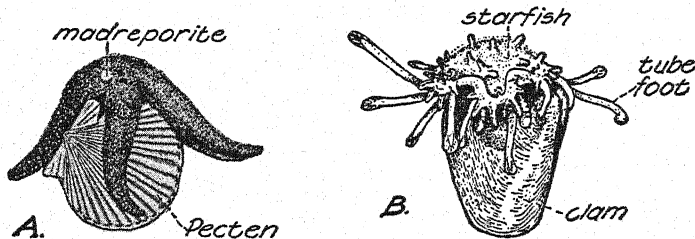


FIG. 400. Starfish feeding on mollusks. A, adult starfish, feeding upon the scallop, *Pecten*. B, very young starfish, feeding upon a clam (cf. Fig. 406 C and D).

(From W. R. Coe, 1912, Connecticut State Geological and Natural History Survey, Bulletin No. 19.)

is effected is still a mystery. One possible explanation is that the starfish secretes a substance which finds its way between the valves and paralyzes the muscles that close the shell of the mollusk. Another is that the tube feet can exert more of a pull than might be expected and perhaps work in relays, so that the muscles of the prey are the first to become exhausted. However the opening may be accomplished, the valves of the mollusk eventually gape sufficiently to admit the starfish's stomach, which is then everted, and so the prey is digested within its shell. The everted stomach may even surround the mollusk completely if it is not too large. In the final stages the stomach is withdrawn, and any remaining fragments of the food are finally digested within the stomach, which has returned to its usual position in the starfish. Small animals, such as snails and crustaceans, may be captured by the tube feet and conveyed to the mouth by bending the arms. Dead or injured animals may also be eaten. Some starfishes, such as *Asterias forreri* of the Pacific Coast, capture crustaceans and even small fishes by holding them with the pedicellariæ until the arms and tube feet can come into action and bring the prey in contact

with the everted stomach (Fig. 401). *Asterias forbesi* and *A. vulgaris* are very destructive to shellfishes. One investigator reported that fifty-six clams, some as long as an arm of the starfish under observation, were devoured by a single starfish in a period of 6 days. On the other hand, a starfish can survive for months without food.

The *digestive system* includes a central *stomach* with so-called cardiac and pyloric regions (Fig. 402). Attached to the pyloric region and extending into the arms are five pairs of branched outgrowths, the *pyloric cæca*, which are digestive glands producing a secretion com-

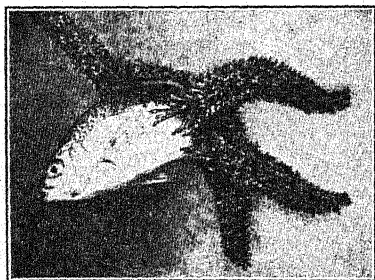


FIG. 401. A starfish, *Asterias forbesi*, feeding upon a fish.

(From H. S. Jennings, 1907, University of California Publications in Zoölogy, vol. 4.)

parable with the pancreatic juice in vertebrates (cf. p. 33). A short *intestine* opens eccentrically on the aboral side of the disk by the *anus*. There is a pair of rudimentary outgrowths from the intestine, called the *rectal cæca*, and presumably homologous with the respiratory trees in holothurians (cf. Fig. 416). *Retractor muscles*, which draw the everted stomach back into the disk, are found in the arms beneath the digestive glands. The spacious cavity enclosed by the body wall and containing the digestive system is the *cælom*. Food

in the last stages of *digestion* may be found in the larger cavities of the pyloric cæca as well as in the central portions of the digestive cavity. *Absorption* occurs by passage of the digested food from the several parts of the digestive tract into the cælomic fluid.

There are vessels encircling the mouth and extending along each arm. Since none of these vessels is pulsatile and since the system is obviously inadequate for the transfer of material in an animal as large as a starfish, they should not be called blood vessels or a circulatory system, as they sometimes are. Their function is problematical. The real mechanism of *circulation* in the starfish, as recently described in detail for *Asterias forbesi*, consists of currents set up by the cilia which cover the surface of the body, the surface of the cælom, and certain other internal cavities. The mechanics of this system can be understood by reference to Figure 405. The cælom contains fluid that is essentially lymph and furnishes the principal means of transferring material in solution from one part of the body to another. The papulæ (Fig. 398), which are hollow outgrowths of the thin body wall between the plates of the skeleton, are *respiratory* and *excretory organs*, by

which exchanges are effected between the cœlomic fluid and the external water.

The *nervous system*, which is radial like other parts of the starfish, is composed of three sets of nerve rings and cords which are not closely

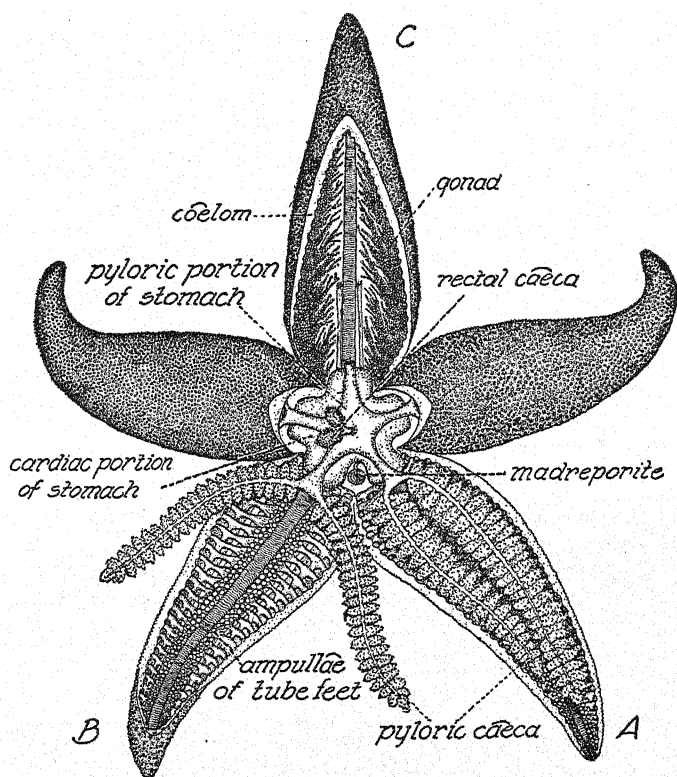


FIG. 402. Internal anatomy of *Asterias vulgaris*, from aboral view. *A*, organs of the cœlomic cavity in their natural positions within the arm. *B*, an arm in which gonads and retractor muscles have been removed and the pyloric cæca separated, showing the ampullæ of the tube feet. *C*, an arm from which the pyloric cæca have been removed, showing the gonads.

(From W. R. Coe, 1912, Connecticut State Geological and Natural History Survey, Bulletin No. 19.)

connected and which contain both nerve cells and their processes (Fig. 403). The *superficial portion* of this system consists of an oral ring from which a radial nerve cord extends along the mid-oral epidermis of each arm. The *deeper portion* includes a double oral ring, from which paired radial nerve cords extend along the oral side of each arm, all

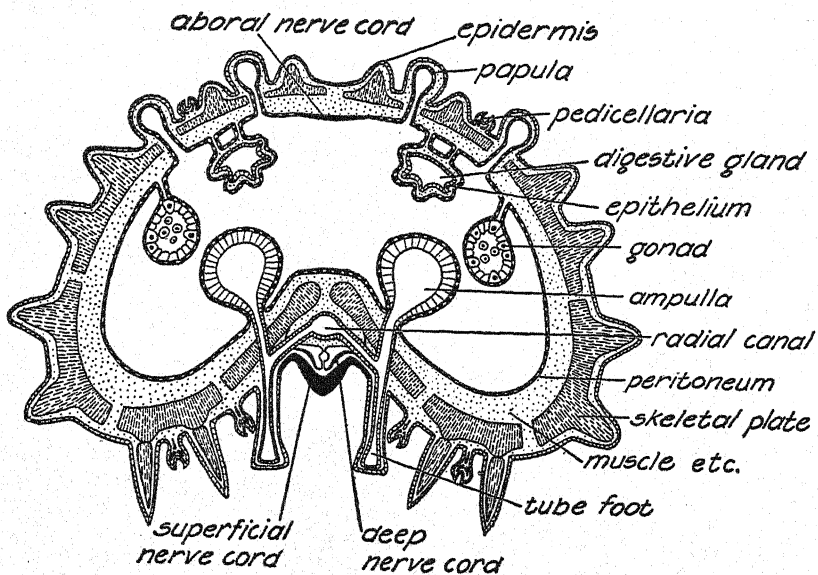


FIG. 403. Transverse section of an arm of the starfish; diagrammatic.

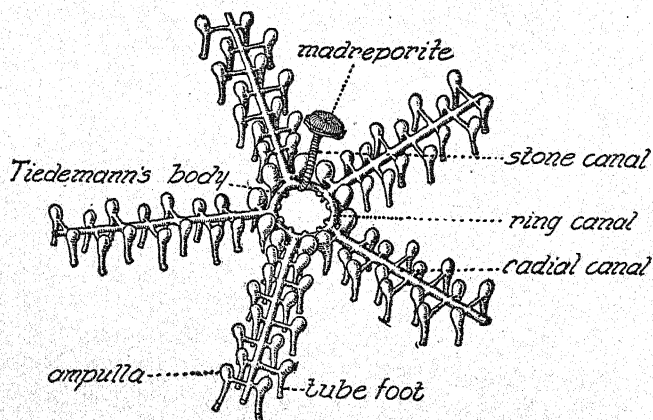


FIG. 404. Water-vascular or ambulacral system of the starfish; diagrammatic.
(From W. R. Coe, 1912, Connecticut State Geological and Natural History Survey, Bulletin No. 19.)

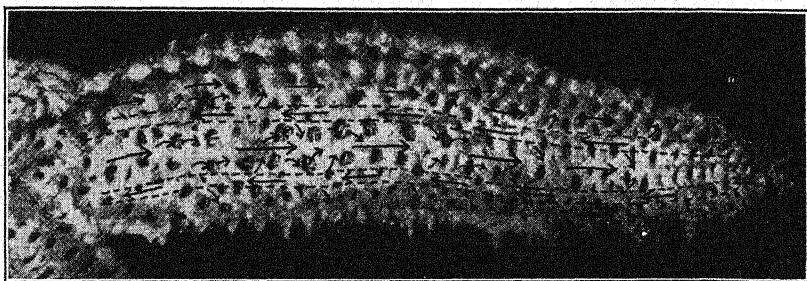
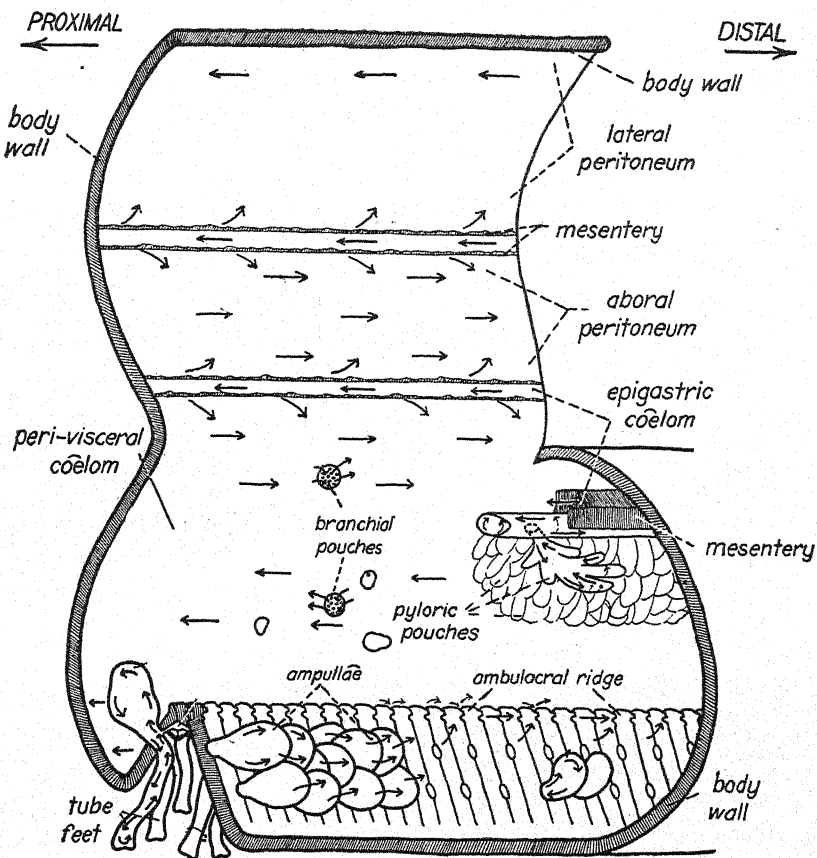


FIG. 405. Ciliary-transport system of the starfish, *Asterias forbesi*. Above, part of an arm with one side cut and reflected upward to show the direction of ciliary currents on the various regions of the peritoneum; diagrammatic. Below, ciliary currents on the aboral peritoneum of one arm; note how these currents dip into and out of the branchial pouches leading to the gills; the dotted lines mark attachments of the mesenteries supporting the pyloric caeca.

(From R. A. Budington, 1942, Biological Bulletin, vol. 83.)

located beneath the epidermis; and an anal nerve ring from which a cord extends along the aboral side of each arm, all located in the aboral peritoneum. There is no obvious centralization of nerve cells anywhere within the nerve rings or cords, and the connections between the three

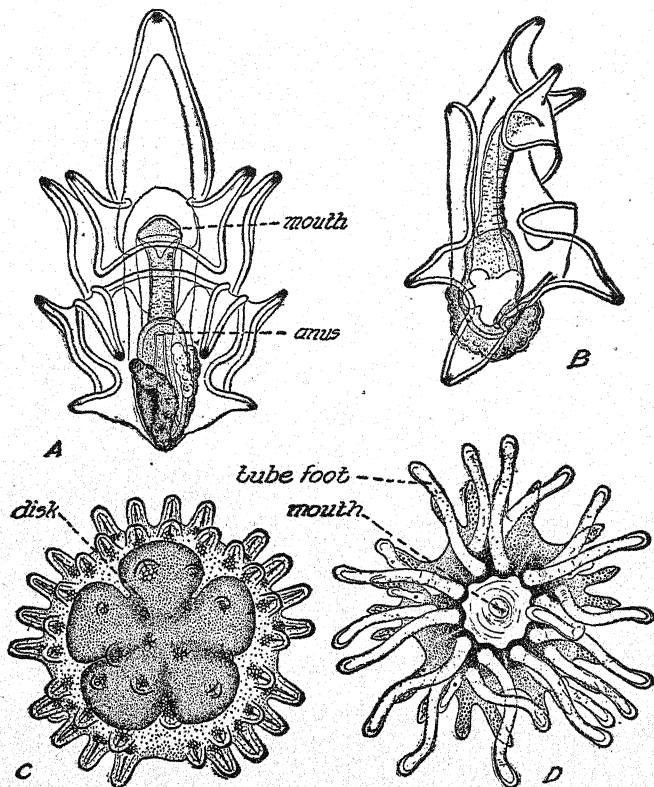


FIG. 406. Development of the starfish. Bipinnaria from (A) ventral and (B) lateral view. Very young starfish from (C) aboral and (D) oral view.

(From W. K. Brooks, "Handbook of invertebrate zoölogy," copyright, 1882, by S. E. Cassino, reprinted by permission.)

systems are obscure. It is presumed that the three systems have structural and therefore functional connections. The remarkable thing is that so limited a nervous system can accomplish the coördination observed in the feeding, righting, and varied locomotor activities (*cf.* Figs. 399-401). *Sense organs* are likewise restricted, although the tube feet seem to have tactile as well as locomotor functions. There are a tentacle and an eye-spot at the end of each arm, and dermal sense organs have been described in other parts of the body.

A unique feature of the anatomy of echinoderms is the water-vascular, or *ambulacral system*, by means of which locomotion is effected (Fig. 404). The madreporite seen on the outside contains the opening of a tube, called the *stone canal*, that leads orally to a *ring canal* about the mouth, from which a *radial canal* passes along the oral surface of each arm. Short, paired, lateral extensions from these radial canals communicate with the *tube feet* and the *ampullæ*, the walls of which are muscular. The fluid is driven into a tube foot by contraction of its ampulla, since there is a valve in each lateral vessel that prevents a backward flow into the radial canal. When the tube foot is extended and attached, contraction of its wall forces the fluid back into the ampulla, thus providing the mechanism for any pull or push against the substratum. This integrated action of the tube feet, as seen in locomotion, is presumably the result of nervous coördination. Apparently the fluid in the ambulacral system may be increased by passage of sea water through the madreporite and may decrease by diffusion through the walls of the vessels into the coelom. The fluid contains amœboid cells produced in the so-called *Tiedemann's vesicles* on the ring canal.

The *skeletal system* is mesodermal and hence an endoskeleton, not an exoskeleton as in the great majority of invertebrate animals. In this respect the echinoderm skeleton resembles that of a vertebrate. The fact that the skeleton of the starfish is composed of many small plates, bound together by muscle fibers and connective tissue, accounts for the plasticity of its body as seen in righting and other activities.

The Reproductive System, Reproduction, and Development. The reproductive system consists of five paired gonads lying free in the coelom of the arms lateral to the pyloric cæca and attached in the angles between arms where their external openings are located (Fig. 402). The sexes are separate; the ova and spermatozoa are discharged

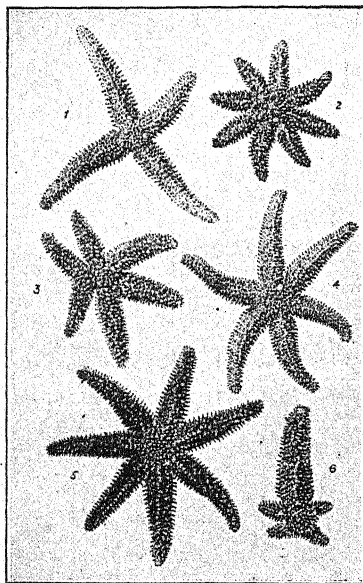


FIG. 407. Starfishes found in nature, abnormal presumably as a result of regeneration after mutilation.

(From W. R. Coe, 1912, Connecticut State Geological and Natural History Survey, Bulletin No. 19.)

through the genital pores into the sea water, where fertilization occurs. Developmental stages include a blastula, gastrula, and the *bipinnaria*, which is a bilateral, ciliated larva that swims near the surface for sev-

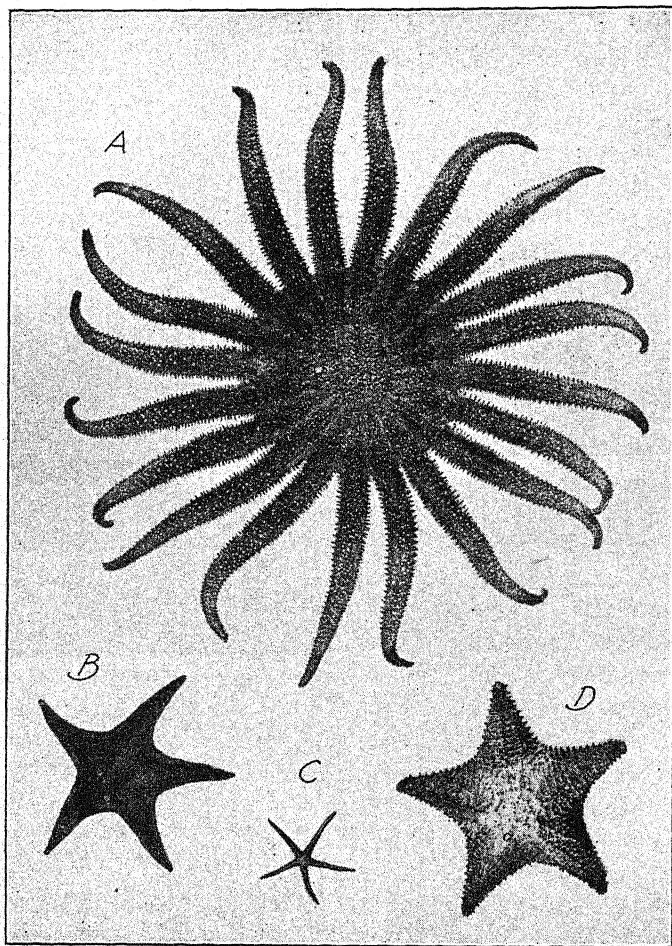


FIG. 408. Representative asteroids, from aboral view. A, *Pycnopodia*. B, *Dermasterias*. C, *Henricia*. D, *Oreaster*.

eral weeks before it settles to the bottom and undergoes metamorphosis to form a miniature starfish (Fig. 406). The occurrence of this bilateral stage in the development of the starfish and other echinoderms suggests that the ancestors of echinoderms were bilaterally symmetrical animals.

Regeneration. Starfish are often found in nature with one or more arms undergoing regeneration (Fig. 407). Under experimental conditions as many as four arms may be removed, and their regeneration will sometimes occur. When all five of the arms are removed, regeneration may still occur if the individual is fed after the formation of the new arms has begun. Although an isolated arm may live for several weeks, it will eventually die, since it cannot restore the disk and other arms. Arms may be broken off by the animal automatically when it is handled. A break of this sort always occurs at the base of the arm, where the coelom is constricted as it passes from arm to disk, and the opening exposed is of minimum area.

Other Asteroidea. In all the members of the Class Asteroidea the body is stellate whether the arms are long and slender, as in *Henricia*, or short and thick, as in *Oreaster* (Fig. 408). In some species more than five arms are present, as in *Solaster* and *Pycnopodia*. In the leather-stars, *Dermasterias*, the skeleton is reduced, and the body is covered with a smooth, spineless skin concealing the underlying skeleton. There are few members of the class so modified that they are not immediately recognizable as asteroids.

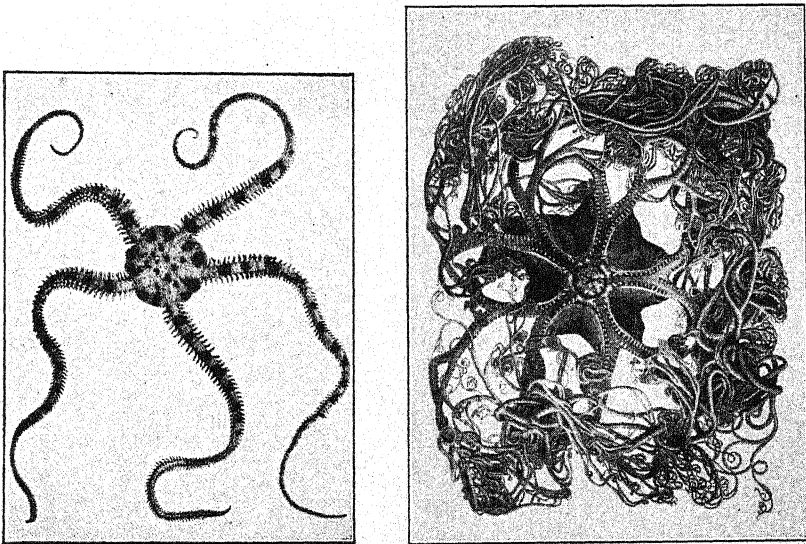


FIG. 409. *Left*, the brittle-star, *Ophiopholis aculeata*, aboral view. *Right*, basket-star, oral view.

(*Left*, from W. R. Coe, 1912, Connecticut State Geological and Natural History Survey, Bulletin No. 19; *right*, photograph of plate from the Prince of Monaco, by courtesy of the American Museum of Natural History.)

The Ophiuroidea

The members of this class, which are called the brittle-stars or serpent-stars, are recognizable by their conspicuous disk and slender, mobile arms (Fig. 409). In one type, called basket-stars, the arms are branched. The volume of the skeleton is relatively greater than in the asteroids, but the organization is clearly that of an echinoderm.

The Echinoidea

The Sea-urchin. A representative of this class is the common sea-urchin, *Arbacia punctulata* (Fig. 410). In contrast with the asteroids

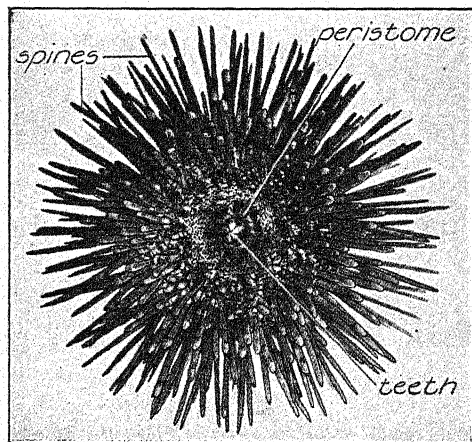


Fig. 410. The purple sea-urchin, *Arbacia punctulata*, oral view.

(From W. R. Coe, 1912, *op. cit.*)

and the ophiuroids, such an echinoid is globular and covered with long movable spines, except in the oral region. *Arbacia* typically inhabits rocky bottoms, where it is found even in exposed places, attached by its tube feet and braced with its spines. Its food consists of seaweeds and small animals. On the oral surface is the *mouth* with five large teeth, surrounded by a *peristome* extending to the margin of the oral opening of the skeleton. There are *pedicellariæ* all over the body, and five pairs of *tentacles* and *papulæ* upon the peristome. The *anus* is in the center of the aboral area surrounded by the five *reproductive openings*, one of which is associated with the opening of the ambulacral system in the *madreporite* (Fig. 411). In the angles between the reproductive openings are *ocular plates*, which lie at the ends of the

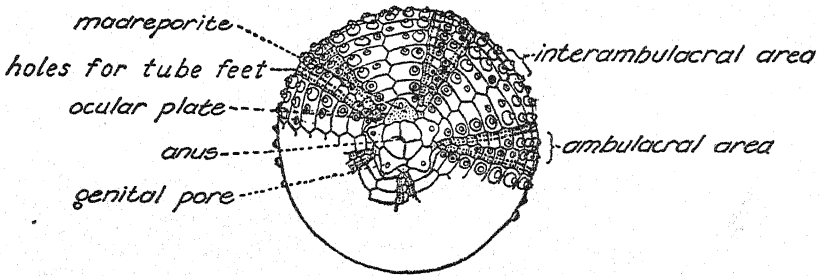


FIG. 411. The test of *Arbacia punctulata*; the spines have been removed, and not all the plates are outlined.

(From W. R. Coe, 1912, *op. cit.*)

ambulacral areas as in the starfish. This complex of aboral structures is associated with special plates of the skeleton. The *tube feet* occur in five double rows along areas that correspond to those of the arms in the starfish and extend from the edge of the peristome to the ocular plates. The remaining external feature of importance is the *spines*, which are movable on ball-and-socket joints and function in locomotion along with the tube feet, as well as for protection. As in the starfish the spines and *test*, or shell-like skeleton (Fig. 411), are mesodermal in origin. The test is composed of many small pieces like the skeletal plates in the body wall of the starfish, but in the sea-urchin the plates fit tightly together. In all existing sea-urchins there are twenty

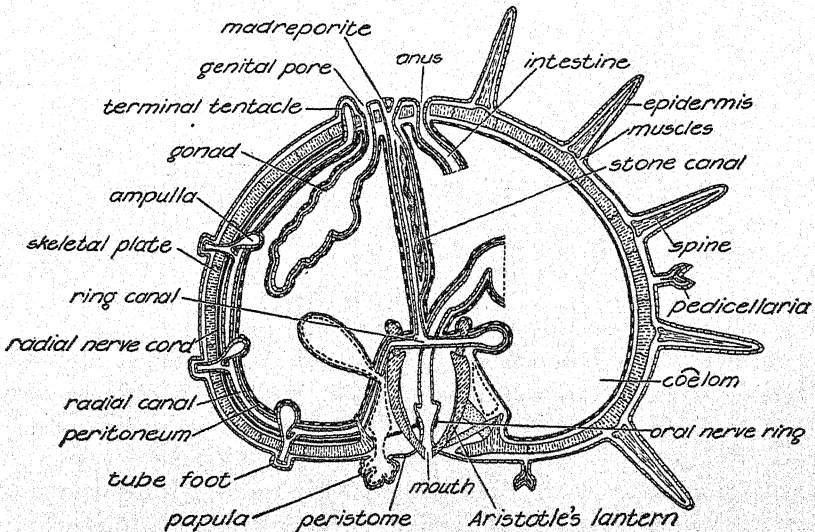


FIG. 412. Vertical section of a sea-urchin; diagrammatic.

rows of these plates, two rows in each ambulacral and two in each inter-ambulacral area of the animal.

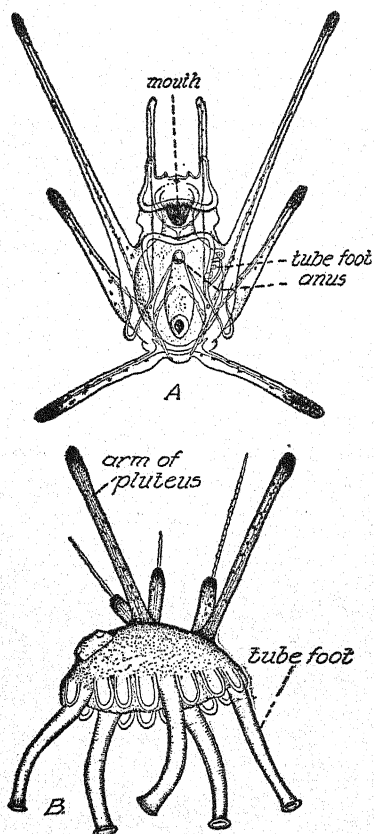


FIG. 413. Development of the sea-urchin. A, pluteus, from ventral view. B, pluteus in metamorphosis, from lateral view, showing the arms of the pluteus in process of degeneration; the oral lobe of the larva is still visible as a protuberance on the aboral surface of the young sea-urchin.

(From W. K. Brooks, "Handbook of invertebrate zoölogy," copyright, 1882, by S. E. Cassino, reprinted by permission.)

When first examined, the *internal organization* seems quite different from that of the starfish (cf. Figs. 402 and 412). The digestive system includes an elaborate organ of mastication, surrounding the esophagus and called Aristotle's lantern, from which the digestive tract extends to the anus as a large tube coiled within the extensive coelom. The circulatory, ambulacral, and reproductive systems, however, are arranged like those of the starfish; the nervous system corresponds to the superficial nervous system of the starfish. The sexes are separate; ova and spermatozoa are discharged from the genital pores. Fertilization thus occurs in the sea water, where development proceeds to a bilateral, ciliated larva, the *pluteus*. This larva is essentially like the bipinnaria of the starfish, although it differs in external structure. After several weeks of pelagic life the pluteus sinks to the bottom, and the metamorphosis to a miniature sea-urchin occurs (Fig. 413). The homologies with the starfish are evident as one studies the sea-urchin more carefully.

Other Echinoidea. In sea-urchins such as *Arbacia* the body is circular in its lateral outline, and the twenty rows of plates are

regularly arranged in a radial pattern. In some early fossil urchins there are no definite rows, since the plates are irregularly arranged. In the type represented by *Clypeaster* the mouth is in the center of the

oral surface, but the anus is on the lateral margin in an interambulacral area so that the animal is bilaterally symmetrical (Fig. 414 B). In the sand-dollar, *Echinarachnius parma*, the organization is like that of the

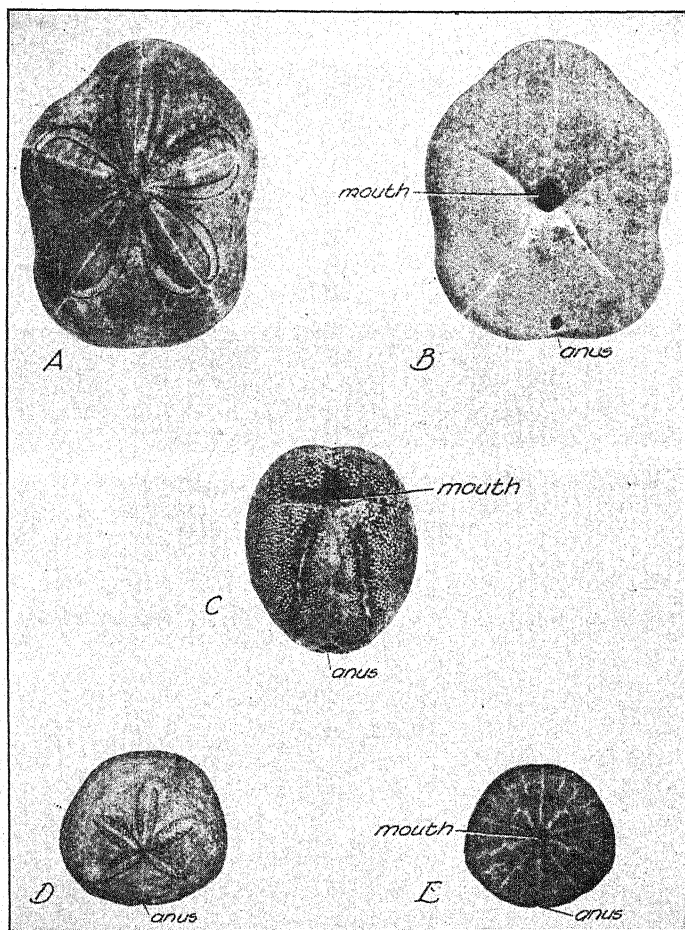


FIG. 414. Bilateral echinoids. A, *Clypeaster*, from aboral and, B, from oral views. C, *Spatangus*, from oral view. D, *Echinarachnius*, from aboral and, E, from oral views.

clypeasters, although much flattened (Fig. 414 E). In the type represented by *Spatangus* the mouth has shifted peripherally, or in an "anterior" direction, along the ambulacral area opposite the anus. (Fig. 414 C). The fossil record and the life-cycles of these bilateral urchins indicate that they have descended from ancestors that were radial like *Arbacia*. The existence of early fossil urchins with an

irregular arrangement of plates suggests that forms such as *Arbacia*, with twenty rows regularly arranged, arose from ancestors without this regularity of the skeleton. It seems clear that the bilateral clypeasters and spatangoids have been evolved from a radial type like the *arbacia*.

The Holothuroidea

The Sea-cucumber. The species *Thyone briareus*, which is a common holothurian of the Atlantic Coast from Cape Cod southward, is a representative example of this type of echinoderm (Fig. 415). The

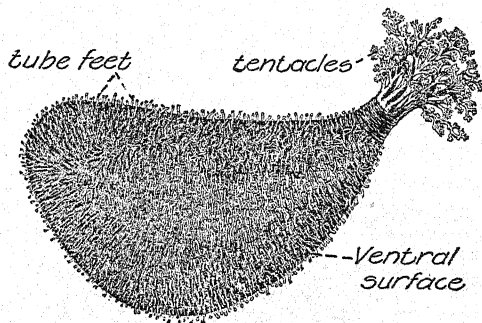


FIG. 415. The sea-cucumber, *Thyone briareus*, lateral view.

(From W. R. Coe, 1912, Connecticut State Geological and Natural History Survey, Bulletin No. 19.)

texture of the body is quite different from that found in the starfish and sea-urchin, since the expanded *Thyone* is soft like a bladder partly distended with fluid, and since there is no skeleton except minute plates of carbonate of lime embedded in the body wall and a few somewhat larger plates in the oral region. The animal lives in the ooze of muddy bottoms just beyond low-tide level. At one end is the *mouth*, surrounded by ten branched *tentacles*, and at the other is the *anus*. The *tube feet* are not in distinct rows but are scattered over the body, although connected with five radial ambulacral canals as in other echinoderms. What may be called the "ventral" surface, since it is directed downward, has larger and more numerous tube feet than the "dorsal" or uppermost surface. Also, the distance from mouth to anus is greater along the ventral midline than along the dorsal. To this extent *Thyone*, when viewed externally, is seen to be bilateral and to be differentiated dorso-ventrally as well as antero-posteriorly.

When embedded in the bottom the animal lies with its anterior or oral end directed diagonally upward with the tentacles outspread.

The anal opening is similarly exposed. If disturbed, the tentacles disappear by inversion of the entire oral end of the body, any excess water is discharged from the anus, and the body becomes tense. In feeding, the tentacles are moved about until well covered with silt from the bottom and are then thrust one at a time deep into the mouth, to be "licked off" as they are withdrawn. The other conspicuous activity

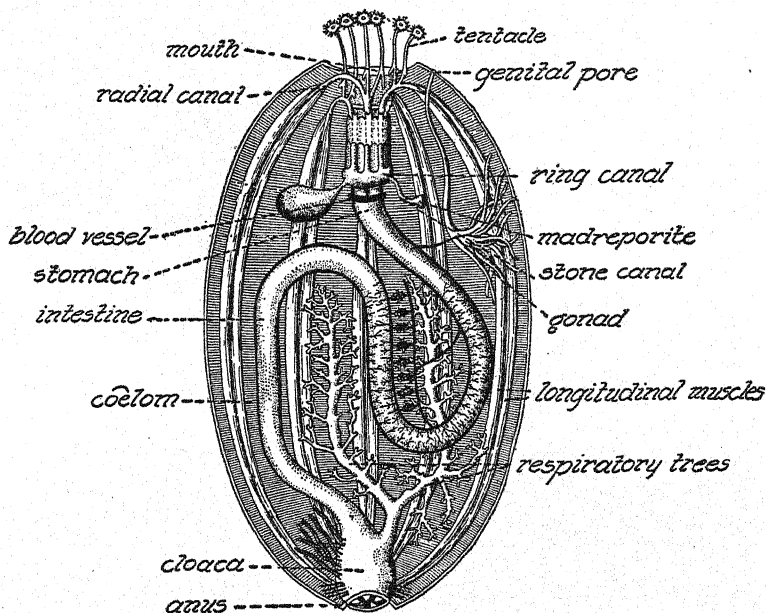


FIG. 416. The internal structure of a sea-cucumber, *Holothuria*; diagrammatic.

(From W. Stempel, "Zoölogie im Grundriss," 1926.)

of the embedded *Thyone* is the pumping of a respiratory current of water in and out of the anus. In locomotion the animal moves by extending its tube feet, attaching the terminal suckers of these organs, and dragging itself along.

Internally, the *digestive system* begins as a short esophagus, which is surrounded, where it enters the coelom, by a skeletonlike structure which supports the tentacles and to which retractor muscles are attached (cf. Fig. 416). The esophagus leads to a stomach, followed by a long, coiled intestine which is attached in part by a mesentery along the mid-ventral body wall. At its posterior end the intestine is enlarged as a cloaca from which a pair of branching structures, the *respiratory trees*, extend into the coelom. These respiratory trees are filled with water drawn through the anus and pumped into them by

contractions of the cloaca. The expulsion of this respiratory water is effected by contraction of the body wall. The only other conspicuous features of the internal anatomy are five longitudinal muscles which lie in the ambulacral areas; the ampullæ of the tube feet, which are scattered over the inner surface of the body wall; and the single *reproductive organ* with its duct, which opens in the dorsal interambu-

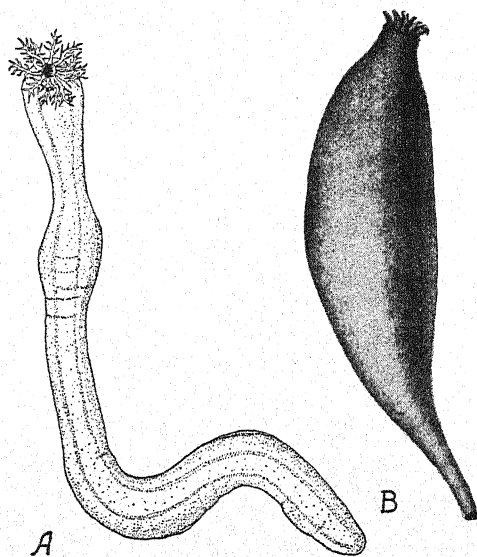


FIG. 417. Holothurians without tube feet. A, *Leptosynapta*. B, *Aphelodactyla*.

(A, from W. R. Coe, 1912, Connecticut State Geological and Natural History Survey, Bulletin No. 19; B, from H. L. Clark, 1916, Smithsonian Contributions, vol. 35.)

lacral area between two of the tentacles. The sexes are separate. Ova and spermatozoa are discharged into the water; development occurs in the open water, as in the majority of echinoderms. As in the starfish and sea-urchin, there is a bilateral larva, called in this instance the *auricularia*. The *ambulacral system* resembles that of the starfish and sea-urchin, except for the stone canal and its madreporite, which hang free in the coelom instead of having an external outlet. The *nervous system* is composed of an oral nerve ring and five radial nerve cords. If the skeleton is disregarded, a sea-cucumber is like a sea-urchin with its body elongated in the axis of radial symmetry, which extends from mouth to anus. Correlated with this are the antero-posterior and dorso-ventral differentiations and the bilateral symmetry of the adult, although the underlying radial symmetry is apparent.

Other Holothuroidea. *Thyone* represents a type of holothurian that is not specialized by any extreme modification of shape or loss of parts. In *Leptosynapta* the tube feet are absent, but there are minute skeletal plates and five muscle bands to be seen externally, which are indicative of the echinoderm organization (Fig. 417 A). Another footless type is *Aphelodactyla* (Fig. 417 B). In *Psolus chitinoides*, a species common on the North Pacific Coast, the dorsal surface is protected by scalelike plates of the skeleton, and the ventral surface resembles the creeping foot of a mollusk save that it has three rows of tube feet (Fig. 419 J).

The Crinoidea

The crinoids, or sea-lilies, are typically forms that live at considerable depths, attached to the bottom by stalks which arise from the

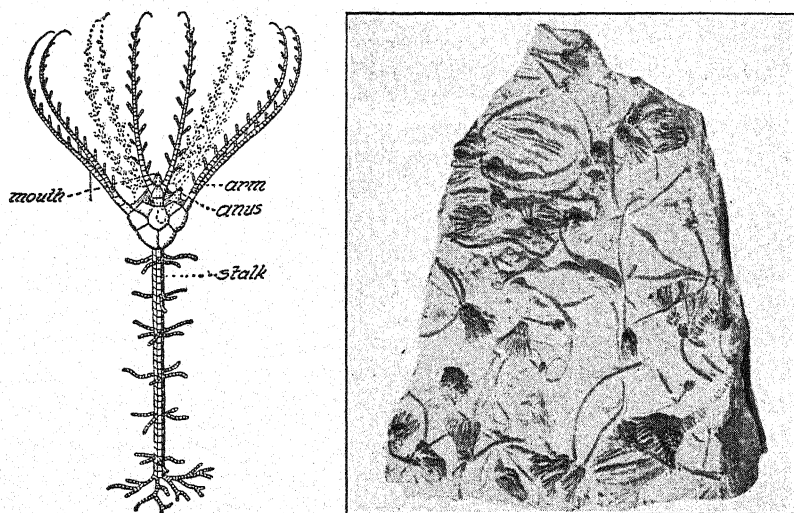


FIG. 418. Crinoids: *Left*, external structure of a crinoid; diagrammatic. *Right*, fossil crinoids in a slab of limestone.

(*Left*, from W. Stempel, "Zoölogie im Grundriss," 1926. *Right*, from photograph by courtesy of Ward's Natural Science Establishment, Inc., Rochester 8, New York.)

aboral region of the body (Figs. 418 and 419 M). The mouth is uppermost in the center of the oral surface and is surrounded by five arms that branch and rebranch. The anus is also found on the oral surface within the circle of arms. Ambulacral grooves, which lie upon the oral surfaces of the arms and which are ciliated, convey the food to the mouth. Tube feet are present, but their function is tactile and to some extent respiratory. Crinoids of the Genus *Antedon* have no stalks and

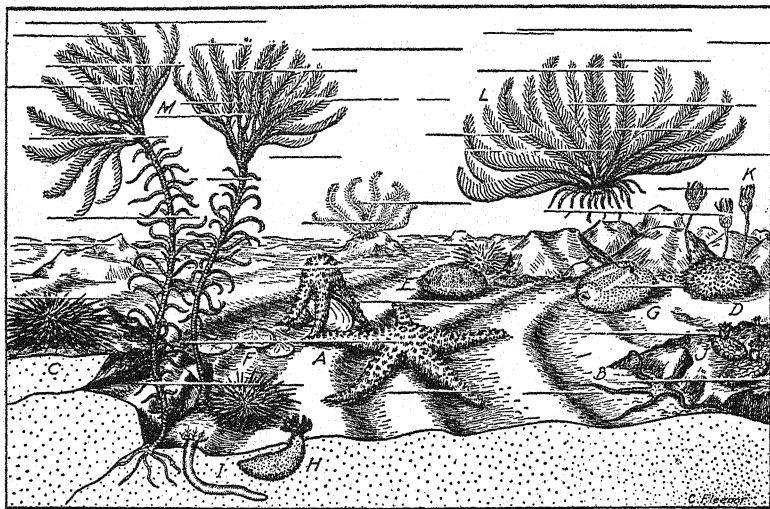


FIG. 419. Representative echinoderms, showing their relations to the substratum without reference to the depths at which they live. A, two individuals of *Asterias*, an asteroid; one of them is feeding upon a clam. B, *Ophiura*, an ophiuroid. C, *Arbacia*; D, *Strongylocentrotus*; E, *Clypeaster*; F, *Echinarachnius*; and G, *Spatangus*: echinoids; only the tests of *Echinarachnius* and *Spatangus* are shown, the latter with oral surface uppermost. H, *Thyone*; I, *Leptosynapta*; J, *Psolus*: holothurians. K, young, attached individuals of *Antedon*; L, adult, free-living *Antedon*; and M, *Metacrinus*: crinoids.

are not attached as adults (Fig. 419 K and L). In the juvenile stages that follow the free-swimming larval stage, they are attached like other crinoids. It is, therefore, presumed that *Antedon* has descended from ancestors attached throughout their adult life, like the great majority of existing crinoids. The existing species of crinoids are few in number as compared with the species of these echinoderms in early geologic times.

The Echinoderm Body-plan

When first compared with the structure found in other Metazoa, the body-plan of an adult echinoderm seems in many respects strange. Upon further examination the adult is found to be triploblastic and coelomate, whereas the larval stages are bilaterally symmetrical. Moreover, the arrangement of tissues in the body wall and in the gut wall of an echinoderm is fundamentally like the arrangement in annelids and vertebrates, as may be seen by comparing a section through an arm of a starfish (Fig. 403) with a transverse section of a frog (Fig. 2, p. 9) and of an earthworm (Fig. 342, p. 461). In each form

the body wall is covered externally by an epidermis and lined internally by peritoneum, and between these two layers are muscular and connective tissues. In each form there is a cœlom lined by a peritoneum which forms an unbroken membrane, except as it may be pierced by excretory or reproductive ducts in annelids and in vertebrates. The digestive tract in each type consists of peritoneum, a region of muscular and connective tissues, and a lining of columnar epithelium. Moreover, all these tissues of body and gut walls arise from the germ layers of the embryo in much the same manner in the worm, the echinoderm, and the vertebrate (*cf.* Fig. 90, p. 149). The worm has no skeleton, and the echinoderm has no excretory and reproductive organs with ducts leading from the cœlom, as in the worm and the vertebrate. The echinoderm has no well-developed circulatory system. All things considered, however, the body-plan of the adult echinoderm seems no longer strange when thus compared with the body-plans found in the other phyla comprising the Eucœlomata (*cf.* Fig. 135, p. 215).

When, in addition, the bilateral larva and its probable significance in evolution are considered, the echinoderm body can be interpreted as an extreme modification of the bilateral-triploblastic-cœlomate plan which appears in all the more highly developed phyla. The structure of the larvæ (bipinnariæ, plutei, auriculariæ, etc.), as found in the several classes of echinoderms, is easily reducible to a generalized larval type, which has been called the *dipleurula*. The question raised by the existence of such a larva is why an animal that is radially symmetrical as an adult should have a bilateral larval stage.

Two answers may be given. Either this larval stage has developed secondarily and represents what happened to be produced in the adjustments of larval life during the long evolutionary history of echinoderms, or it occurs in the development of echinoderms because it represents something in their ancestry, in the same manner as the fishlike stages in the development of higher vertebrates (*cf.* p. 670). Those who regard the *dipleurula* as representing a bilaterally symmetrical ancestor of echinoderms would suppose that this ancestor became attached and acquired a five-parted radial symmetry. Most of the crinoids have persisted in this attached stage, whereas the ancestors of asteroids, ophiuroids, echinoids, and holothuroids gave up attachment and have become variously modified for free life. Echinoderms such as some of the holothurians and sea-urchins, which are bilaterally symmetrical as adults, have assumed a new bilaterality which has no relation to that found in their larvæ. If this represents the "grand course" of evolution in echinoderms, it takes us a long way into the past, since the present classes of echinoderms existed in the Cambrian Period, when fossils first appear abundantly in the rocks (*cf.* Fig. 469, p. 646).

CHAPTER 18

THE ORGAN-SYSTEMS OF INVERTEBRATES

The organ-systems of vertebrates have been described in Chapters 2 and 3. In subsequent chapters certain comparisons have been drawn between these systems in vertebrate and in invertebrate animals. In this chapter an account of invertebrate organ-systems is presented in more general terms. Such an account will illustrate the kind of variety and unity that is everywhere apparent when one looks carefully at the world of animal life. In some cases the plan of an organ-system is remarkably similar throughout a considerable number of phyla. In others the structural relationships in different phyla are such that the systems in these phyla are clearly not homologous, although the functions of non-homologous parts may be analogous. Examples of this sort illustrate the fact that animals have certain basic necessities of existence and that, to speak figuratively, they have solved their problems in a variety of ways. For example, the metabolism of the animal imposes certain general requirements which are met by the many reactions involved in the capture, ingestion, digestion, circulation, and assimilation of food; and these reactions tend to become more elaborate with an increasing size and complexity. Animals ingest many kinds of food, and their digestive systems are correspondingly adapted to their individual necessities. And yet there are obvious similarities in the digestive systems of animals that have digestive tracts. In fact, the digestive system has much the same fundamental structure in all animals that have both mouth and anus. By contrast, the reproductive systems of the different phyla show great diversity of structure. In many instances, when comparisons are made among these organs in animals belonging to different phyla, it is clear that they are not homologous. Nevertheless, there are remarkable parallels in the functions. The problem of developing an efficient reproductive system has been solved in a great variety of ways. Finally, such a review as will be undertaken in the present chapter furnishes data for consideration by the student of evolution, although little reference will be made to this aspect of the subject.

Since the references to figures and specific items in previous chapters are very important for an understanding of the discussion, the student should be careful to look up each such reference as it is given and keep these scattered items in mind.

Systems Related to Metabolism

Digestive Systems. The structures and activities related to the ingestion and digestion of food by Protozoa should be recalled for comparison with what occurs in the various phyla of invertebrates. In such a protozoan as the paramecium (*cf.* p. 260) there is a cytostome,

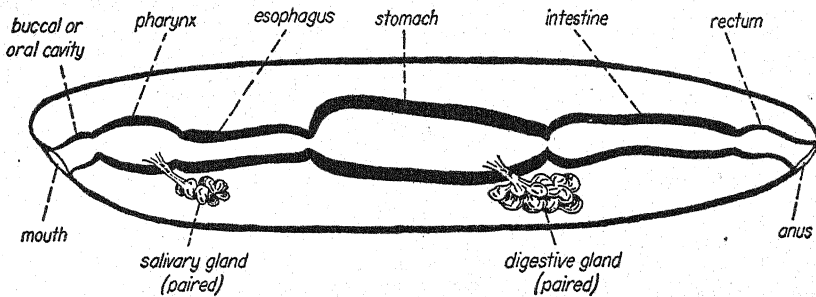


FIG. 420. The invertebrate digestive system; schematic.

or cell mouth, a gullet, food vacuoles, sometimes called "temporary stomachs," and an anal spot, where egestion occurs. Some protozoans have a more elaborate mechanism for capturing food and conveying it to the cytostome than does the paramecium. In the Mesozoa and the Porifera there is no enteron, or digestive cavity. In the Cœlenterata, Ctenophora, and Platyhelminthes, the enteron is a cavity rather than a "tract," if one defines a digestive tract as a pathway along which food moves from mouth to anus. In the other phyla of invertebrates there is, typically, an enteron with both mouth and anus, and so the term digestive tract is applicable. It is interesting to note that in some protozoans there is a tractlike course which is taken by the food as it traverses the single-celled animal (*cf.* p. 264). The intracellular digestion, which occurs in Protozoa and in the digestive and certain other cells of Metazoa, presents another parallel between single-celled and many-celled animals.

As we pass on to the invertebrates that have an enteron with both mouth and anal openings, comparisons may be made by means of a generalized diagram (Fig. 420). This figure is a schematic representation of an invertebrate digestive system having all the important

parts that might be found in a single species. Certain invertebrates have all these parts, but in most species some of them are missing. The digestive systems of animals are adapted to many different kinds of food and therefore to many ways of feeding and the related needs of digestion. Parts that are necessary for ingestion and digestion in some species may be unnecessary in others and so may be absent or reduced even in species within the same phylum, as may be illustrated by the jaws of the clamworm (p. 443) and the lips of the earthworm (p. 448). The digestive systems of forms described in preceding chapters may be effectively reviewed by comparisons with the schematic figure. For example, the parts of the digestive systems and their functions in the animals listed below may be compared with the figure. The related textual accounts should be consulted as well as the figure references.

Rotifer (Fig. 262, p. 374)

Roundworm (Fig. 272, p. 385)

Bryozoan (Fig. 287, p. 400)

Sipunculoid (Fig. 292, p. 407)

Mussel (Fig. 298, p. 415)

Squid (Fig. 325, p. 439)

Earthworm (Fig. 332, p. 449)

Crayfish (Fig. 348, p. 473)

Water-flea (Fig. 352, p. 480)

Locust (Fig. 360, p. 490)

Starfish (Fig. 402, p. 541)

Sea-cucumber (Fig. 416, p. 553)

With respect to functions, the mouthparts, mouth cavity, and pharynx function in *ingestion*, the esophagus is a passageway, the stomach is the place where *digestion* and *absorption* begin, the intestine is a region where absorption is completed, and the terminal region called the rectum may have special functions. Salivary glands secrete digestive enzymes or merely lubricating fluids. A digestive gland opening into the region between stomach and intestine commonly supplies the principal digestive juices. Unicellular glands which secrete lubricants or enzymes may also occur throughout the tract. As in the vertebrate, absorption consists in the passage of digested food through the lining of the tract into any blood or lymph spaces in its wall or directly into the body cavity. The parallel with structure and function in the vertebrates is obvious, and so the digestive mechanism is much the same in all animals that have a digestive tract with mouth and anus.

Circulatory Systems. The circulatory systems of invertebrates are more diversified than are their digestive systems. The circulation of food vacuoles in Protozoa brings the food and later the nutrients resulting from digestion in close contact with all regions of the cell. Although it is not the circulation of an internal bloodlike fluid, the passage of water through the canal systems in the Porifera furnishes a transportation system for incoming food and outgoing excretions

(cf. Fig. 201, p. 304). In the Cœlenterata and Ctenophora no blood system is necessary because the digestive cavity extends throughout the body (Fig. 421 A). No parts are far removed from the nutrients resulting from digestion in the enteron, except such tentacles as have

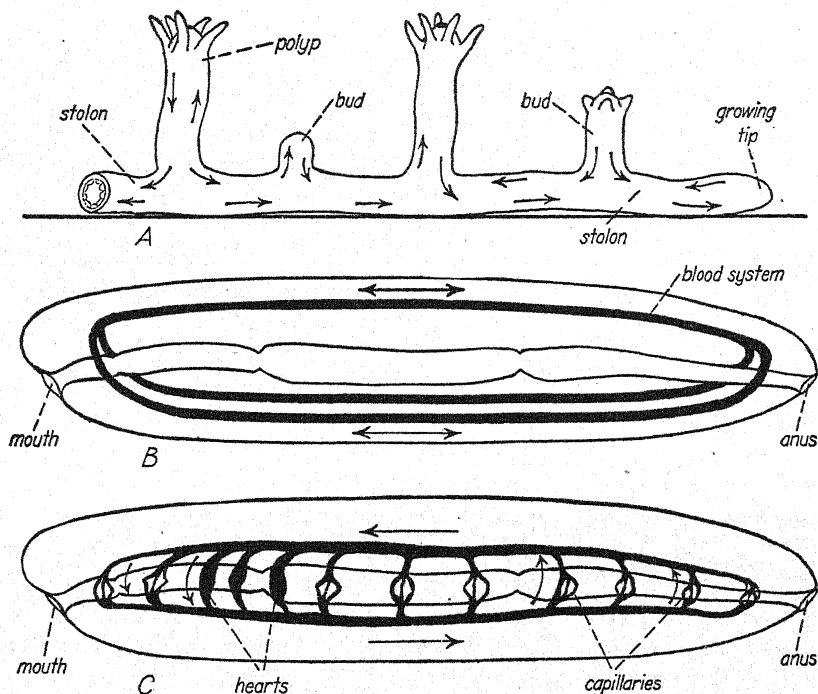


FIG. 421. Invertebrate circulatory systems; schematic. A, circulation within an enteron, which extends to all parts of the body (Cœlenterata). B, blood vessels without pulsatile walls; blood driven back and forth by movements of body (Nemertinea). C, blood vessels extensively developed; larger vessels pulsatile, some of them called "hearts"; the blood thus flows in a definite course (Annelida).

a solid core of endoderm cells instead of an extension of the enteron, as in the hydra. Because the food thus circulates in an enteron extending into all parts of the animal, the gut cavity of cœlenterates is sometimes called a *gastro-vascular cavity*. The Platyhelminthes, which have no anal opening and in which the gut branches likewise extend throughout the body, present a similar relationship in bilaterally symmetrical animals. In the Nemertinea, which have an anal opening and a digestive tract comparable with those in the schematic Figure 420, there are so-called blood vessels, although there seems

to be no mechanism of circulation other than the movements of the animal's body, which presumably result in movements of the fluid within these vessels (Fig. 421 B).

In a system having a definite circulation, the simplest mechanism for making the blood flow is the peristaltic contraction of the principal vessels (Fig. 421 C). This may be illustrated specifically by the blood system of the earthworm (*cf.* Fig. 334, p. 452), in which the larger vessels are contractile and so drive the blood along a definite course. The "hearts" of the earthworm are merely local enlargements of certain vessels. The *heart*, which is found in all well-developed circulatory systems, probably arose in evolution by specialization of a contractile vessel.

There are two main types among the well-developed invertebrate circulatory systems. In one, called the *closed system* (Fig. 421 B and C), the blood is always enclosed within vessels that are continuous through a circuit of heart, arteries, capillaries, and veins, as the vessels may be termed in the fully developed systems of this sort. These systems are found in the Annelida and in such mollusks as the squids. They resemble the circulatory systems of vertebrates to the extent that they are closed systems with hearts. More common among invertebrates is the so-called *open system* (Fig. 422 B and C). A specific example is the pelecypod mollusks (*cf.* Fig. 299, p. 417). In these animals the blood flows from the heart through arteries to all parts of the body and then flows from the smallest branches of the arteries, not into capillaries leading to veins, but into the intercellular spaces of the meshlike mesodermal tissue. There are no capillaries unless the vessels of the nephridia can be so designated. From these intercellular spaces the blood enters the smallest branches of the veins and so returns to the heart. Arthropods such as the crayfish (Fig. 348, p. 473) have a system of this sort in which arteries extend to all the parts, but there are no veins other than large sinuslike spaces and certain tubular vessels. In insects (Fig. 422 C) the relationship is even simpler because there are no arteries except as the anterior extension of the heart is so called (*cf.* Figs. 362 and 363, pp. 492 and 493). In crustaceans such as the water-fleas (Fig. 352, p. 480) there is a conspicuous heart, but the arteries are even less developed than in the insect. A unique feature of the arthropod system is the way in which blood enters the heart through perforations of the heart wall, called *ostia* and guarded by valves (Fig. 422 C). In some of the Tracheata, or air-breathing arthropods, the circulation is aided by a diaphragmlike membrane just ventral to the heart (locust) and another in the ventral body region (honey-bee). It will be recalled

that the oxygen-carrying function is performed not by the circulatory system but by the tracheæ, or air-tubes, of these arthropods. In other invertebrates the heart, if present, may consist only of a thick-walled contractile portion, the *ventricle*; or there may be, in addi-

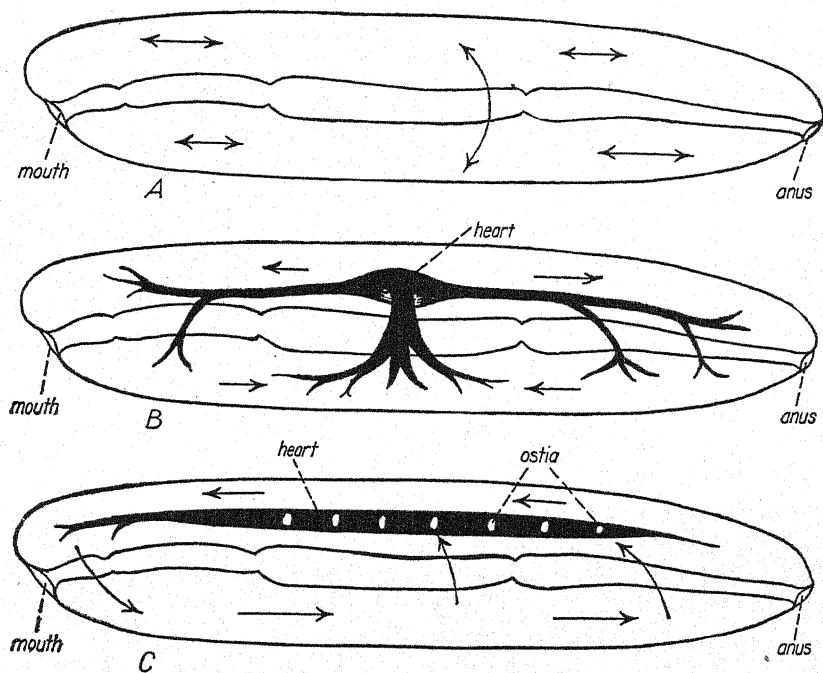


FIG. 422. Invertebrate circulatory systems; schematic. *A*, no blood except the fluid in body cavity, which is driven back and forth by movements of the animal (Nematoda). *B*, a heart consisting of right and left auricles and a single ventricle forces the blood through arteries, from which it passes into the intercellular spaces throughout the body and thence to veinlike vessels leading to the auricles (Pelecypoda). *C*, a heart consisting of a tubular vessel with paired lateral openings (ostia), through which the blood enters the heart; the blood flows anteriorly into the intercellular spaces (hemocoels), from which it eventually enters the ostia (Insecta).

tion, *auricles*, or *atria*, which are thin-walled and act as reservoirs from which the blood passes into the ventricle during its expansion.

Examples of well-developed and representative circulatory systems among the invertebrates are thus found in the Annelida, the Mollusca, and the Arthropoda. The effective though simple circulation of echinoderms is unique (*cf.* Fig. 405, p. 543). Circulatory systems are absent or but slightly developed in the other phyla of the invertebrates. What

has been stated regarding the general functions of the circulatory system of the vertebrate (*cf.* pp. 52-54) is applicable in each of these cases. Typically, the circulation of the invertebrate brings nutrients and oxygen to the cells and carries away the end products of metabolism.

Respiratory Systems. Special organs of respiration are not commonly found among invertebrates in which an intake of oxygen is possible over a considerable part of the body surface (*cf.* the hydra and earthworm). Among the invertebrates that do have respiratory organs there is a bewildering diversity, although these organs can be

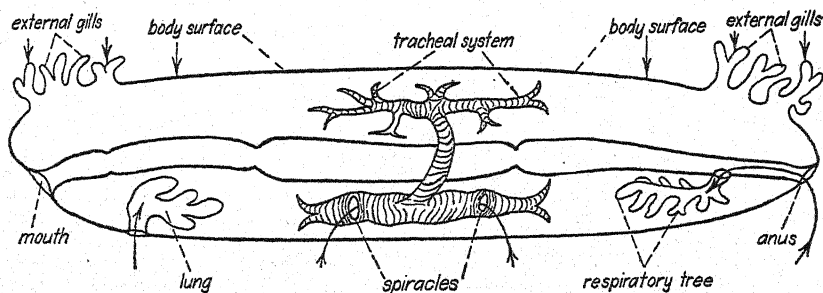


FIG. 423. Invertebrate respiratory systems; schematic and composite.

classified into a few general types (Fig. 423). For example, there are outgrowths of the external surface which are essentially *external gills* (*cf.* Fig. 321, p. 434), although not always called gills. There are *internal gills*, such as those of the fresh-water mussels (*cf.* Fig. 297, p. 414), which are contained within cavities, although they are outgrowths of the external surface. There are cavities called *lungs*, which open externally and are likewise part of the external surface, as in the land snails and slugs (p. 434). And, finally, there are the *tracheæ*, or air-tubes, of insects and related arthropods.

Aside from some very special exceptions, such as the respiratory trees of holothurians (Fig. 416, p. 553) and of certain other echinoderms, all respiratory organs of invertebrates may be placed in one of these general types. The essential relationships are similar in all these cases; namely, a thin layer of cells separates the blood or body fluid of the animal from external water or air that is well supplied with oxygen. The relationship is thus the same as in the gills and the lungs of the vertebrate (*cf.* p. 48). Moreover, an outgo of carbon dioxide is usually associated with the intake of oxygen in the invertebrates, as it is in vertebrates. The *external respiration* effected by gills, lungs, and air-tubes is likewise to be distinguished from the *internal respira-*

tion, whereby the cells of the invertebrate receive and use oxygen in relation to dissimilation. There are no special organ-systems related to anærobic respiration (*cf.* p. 384), which is, presumably, a process involving the chemical changes of dissimilation within the cells of an animal that obtains oxygen by this method.

Excretory Systems. A comparison of excretion in Protozoa and Metazoa has been made, and the functions of contractile vacuoules considered (*cf.* p. 248). It will be recalled that excretory organs are not found in sponges, coelenterates, and ctenophores. In these animals it is supposed that excretion, like respiration, can occur at any portion of the surface that is freely exposed to the external water (Fig. 426). In addition it has been found in some sponges and coelenterates that the cytoplasm of certain amœboid cells becomes filled with minute particles which seem to be excretory products. Eventually these cells migrate to the outer surface of the animal, become detached and disintegrate, and so remove the excretory products contained. In other coelenterates it appears that excretory material accumulates and is stored indefinitely as the particles found in certain cells (*cf.* Fig. 424). In a few coelenterates there are localized regions in which particles accumulate or from which they are discharged. Although the chemical nature of such particles has not been ascertained in many of these cases, it is thought that they originate as end products of metabolism comparable with the excretory products of higher animals. The accumulation and discharge of such products in a particular part of the body suggest the beginnings of specialized excretory regions or organs.

In the echinoderms there are no special organs of excretion, unless the respiratory papillæ or "gills" have excretory as well as respiratory functions. In addition to the excretion by diffusion of wastes in solution, which certainly occurs in echinoderms, at least some members of this phylum have amœboid cells that collect and then discharge a variety of particles (*cf.* Fig. 424). For example, when India ink granules are introduced into the coelom of the starfish, they are engulfed by such cells, which migrate to the respiratory papillæ and disgorge their contents. The ink is then discharged into the external water by local ruptures of the papillæ. In like manner, colored particles which are believed to be excretory matter are collected and discharged in the normal animal. A similar process occurs in the papulæ of sea-urchins (*cf.* Fig. 412, p. 549) and in the respiratory trees of sea-cucumbers (*cf.* Fig. 416, p. 553). Excretion by storage of waste products in certain cells also seems to occur in some echinoderms. The elaboration of such modes of excretion in echinoderms

may be correlated with the absence of any system of blood vessels adequate for the needs of these animals and the existence of a highly developed circulation of the coelomic fluid (Fig. 405, p. 543).

Other examples of excretory functions exhibited by individual cells or tissues, in contrast to special organs, could be cited from the invertebrates, notably the chloragogue cells of earthworms (*cf.* Figs. 424 and 425 A). Organs believed to be excretory are found in most species

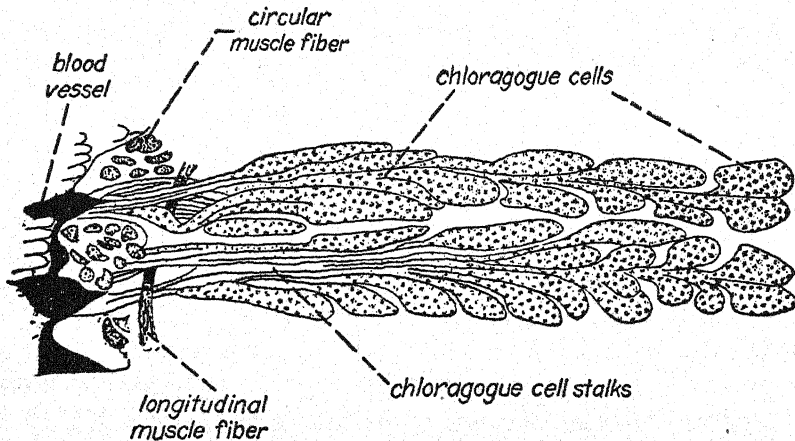


FIG. 424. Chloragogue cells of the earthworm (*cf.* Fig. 342, p. 461). These are modified peritoneal cells containing an accumulation of granules, supposed to be excretory material.

(Modified from C. G. Rogers, "Textbook of comparative physiology," copyright, 1927, by McGraw-Hill Book Co., printed by permission.)

of the other invertebrate phyla, beginning with the flatworms. In contrast to the diversity of respiratory organs these excretory organs have a high degree of uniformity and may in fact be grouped as two types having certain features in common and known as *protonephridia* and *nephridia* respectively.

Protonephridia are best represented in the Platyhelminthes (Fig. 240, p. 351). They consist of systems of vessels beginning as the so-called flame cells or bulbs, from which tubules extend and unite to form larger vessels having one or more external openings. In addition to the tufts of cilia contained in the bulbs and called the "flames," there are cilia at intervals in such a system of tubules, if not along the entire length. The lesser branches are intracellular ducts, but the larger ones may be intercellular. The minuteness of these systems and their internal location have made them difficult to investigate. It is believed, largely because of their structure, that soluble excretory

matter passes from the tissues into the tubules by way of the flame cells and that the cilia make the fluid within the tubules flow toward the external openings. The most typical protonephridia are found in such invertebrates as the platyhelminths, which have no body cavity of any sort. What seem to be very specialized protonephridia are found in Nemertinea, Nematoda, and some other groups among the simpler invertebrates.

The excretory organs called *nephridia* (Fig. 335, p. 453) are characteristic of the Coelomata, or invertebrates having a coelom (*cf.* Fig. 135, p. 215). Like protonephridia, they are composed of tubules, which may be in part intracellular ducts, although the ducts of nephridia are mainly intercellular. More important differences are found in the relationships of nephridia to the coelom and to the reproductive organs. If the animal is non-metameric, like a mollusk, there is typically a single pair of nephridia; if it is metameric, like an earthworm, a pair of nephridia may be found in almost every somite. However, in most of the arthropods, which are metameric animals, the nephridia seem to have been lost or greatly modified.

The nephridia of the fresh-water mussel (Fig. 298, p. 415) are representative of these organs in a non-metameric invertebrate. Here, the nephridium consists of a tube opening at one end from the pericardium, which is the coelom of this mollusk, and opening at its other end into one of the suprabranchial cavities, which is in reality a part of the outer surface of the animal. The funnel-like opening that leads from the coelom is ciliated, and cilia are found in other parts of the tubule. In the mussel the nephridium is bent upon itself and differentiated into an inner glandular and an outer bladderlike portion. The glandular portion is well supplied with blood vessels. Thus, the nephridium is a tube leading from the coelom to the outer surface of the body. In the fresh-water mussel and other pelecypods there is no relationship between nephridia and reproductive organs; in some other mollusks such a relationship exists. A connection with the coelom, as found in the mussel, is typical for the Mollusca.

The nephridia of such an annelid as the clamworm (*cf.* Fig. 427 D) are representative of these organs as found in metameric animals. In the earthworm the nephridium consists of a long tubule, opening at one end from the coelom by a ciliated funnel and opening at the other end upon the external surface of the worm. The tubule is differentiated into several regions, including a terminal, bladderlike portion; in some of these regions the cavity of the tubule is ciliated. Capillaries of the blood system are interlaced with the folds of such a nephridium. Hence, the nephridium of the earthworm, like that of the mussel, is a

tube leading from the coelom to the outside. In the clamworm (cf. p. 444) the nephridia serve also as reproductive ducts, through which the ova and spermatozoa are discharged. The reproductive ducts of such an annelid as the earthworm are probably nephridia that have

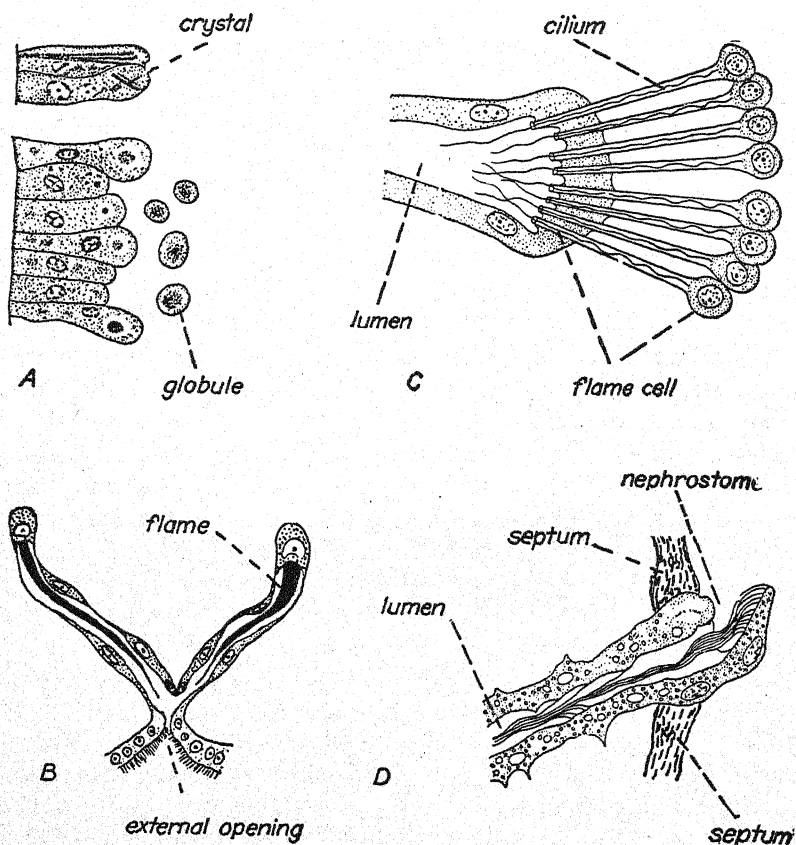


FIG. 425. Excretory mechanisms. *A*, excretion by detachment of globules from certain cells, as in lobster. *B*, protonephridia of *Pedicellina cernua* (cf. Fig. 285, p. 397). *C*, flame bulb of the annelid *Phyllodoce paretii*, consisting of many cells and here shown in section. *D*, nephrostome of a nephridium in the annelid *Trypanosyllis*, in section.

(*A*, *C*, and *D*, modified from C. G. Rogers, *op. cit.*, printed by permission. *B*, from J. Cori, in W. Kükenthal, "Handbuch der Zoologie.")

been specialized for this purpose in the course of evolution. Although most annelids have nephridia with ciliated funnels leading from the coelom, as in the earthworm, some annelids have nephridia that terminate internally in flame cells or bulbs (Fig. 425 C) and hence have

excretory organs that can be called protonephridia. Cases of this sort suggest that nephridia with funnels may have arisen by evolution from protonephridia. In some representatives of the minor invertebrate phyla (*cf.* Chapter 13) that have nephridia these organs consist of a single pair of ciliated tubules leading from the coelom to the outside and usually functioning as reproductive ducts in addition to being excretory organs. In other cases the excretory system consists of a single pair of flame cells and their ducts (*Fig. 425 B*).

In the great majority of the Arthropoda it appears that most of the nephridia, which might be found as a pair to a somite in a metameric

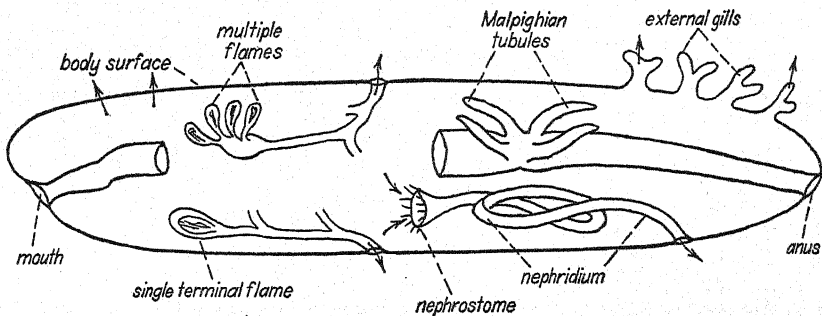


FIG. 426. Invertebrate excretory systems; schematic and composite.

invertebrate, have been lost or greatly modified; and the coelom of most arthropods is so reduced that it is problematical. The probable evolution of arthropods from annelidlike ancestors and the rudimentary coelom and nephridia found in Onychophora (*cf.* Fig. 390, p. 527), suggest that a well-developed coelom and paired nephridia for each somite have been lost or greatly modified in the evolution of this phylum.

Although nephridia seem to be excretory organs, the exact manner in which they function has not been fully established, if, indeed, all nephridia function in the same manner. This uncertainty is not surprising, since the functioning of the kidney tubules in vertebrates (*cf.* p. 52) was long in dispute, despite the many investigations upon the kidneys of these animals. The structure of the nephridia is such that fluid and even particles from the coelom could be discharged by way of these organs. The relationship between nephridia and blood vessels, in animals having nephridia and a well-developed blood system, is such that material in solution could be discharged from blood vessels into nephridia or from nephridia into blood vessels. The extent to which such discharges occur and the exact way in which nephridia function as excretory organs remain to be determined for each phylum. The

structural relationships of nephridia to the coelom and to the reproductive organs of invertebrates has been much discussed by comparative anatomists. Whatever the uncertainties in these relationships, it ap-

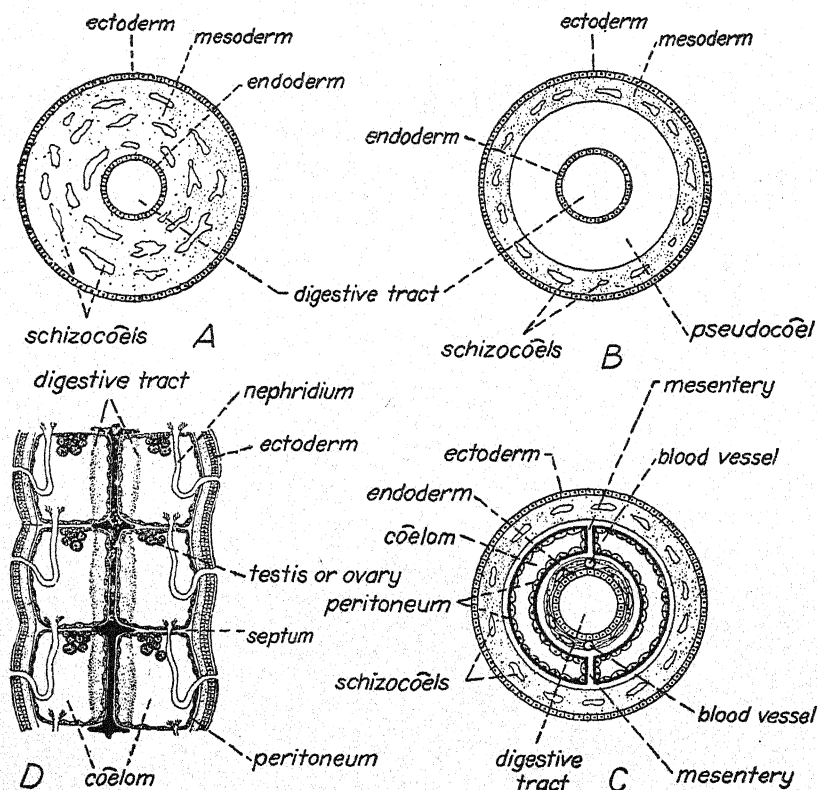


FIG. 427. Body cavities of invertebrates: schizocoels, pseudocoel, and coelom. The relationship of reproductive organs and nephridia to the coelom is shown in D.

(Modified from W. Stempel, "Zoölogie im Grundriss," 1926.)

pears that the nephridia, the coelom, the reproductive organs, and the reproductive ducts have been intimately related in the evolution of these animals. The schematic Figure 426 shows the more important types of excretory surfaces and related organs among invertebrates.

Systems Related to Irritability

The nervous mechanisms by which the reactions of invertebrates are coördinated have been described in such representative animals as the

hydra and the earthworm. In addition to these mechanisms of nervous coördination it appears that many invertebrates produce substances which are transported in the blood or body fluids and bring about endocrine coördinations. The dual mechanism that has been described at some length for the vertebrates (*cf.* Chapter 3) thus extends throughout the Animal Kingdom.

Endocrine Organs and Secretions. Within the past 20 years it has been shown in an increasing number of cases that certain organs or tissues of invertebrates secrete what can be called endocrines, or hormones, because of their action within the animal producing them. For example, there seem to be sex hormones which affect the secondary sexual characters in certain gastropod and cephalopod Mollusca and in certain Crustacea. Other hormones seem to influence the transformation from larval to pupal stages in Diptera and perhaps in other Insecta, and hormones may be important factors in the change from pupa to adult and in the molting of insects. In like manner the color changes of crustaceans and insects are influenced, if not wholly controlled, by hormones. Many other instances could be cited. The widespread production of hormones in the invertebrates can no longer be questioned, although there are many conflicting accounts in the recorded observations and experiments, as must be expected in the initial period of any extensive investigation. Some of these invertebrate hormones resemble the hormones of vertebrates in their chemical nature and, when used in experiments upon vertebrates, produce effects that might have been expected. And, conversely, it has been shown that vertebrate hormones may affect invertebrates, sometimes in ways that are comparable to the effects of the hormone upon the vertebrate. The investigation of hormones in the invertebrates is just beginning, despite the many publications in this field.

Sensory-neuro-motor Systems. The reactions of Protozoa illustrate the fact that all protoplasm responds in some degree to stimulation. It will be recalled that certain protozoan cells exhibit much greater complexity of cell structure than any cells of Metazoa. In like manner some protozoan cells exhibit more complex responses than any single metazoan cells. Moreover, the sensory cilia, conductile fibrils, and contractile fibrils, as found in some protozoan cells (Fig. 176, p. 266), parallel the reception, transmission, and effector mechanisms to be found in metazoans.

In the Porifera (*cf.* p. 307) the only reactions to stimuli which can be easily demonstrated are the closing of pores and oscula and the slight contractions of the entire sponge with a slow return to the expanded state. In correlation with these limited responses the only

cells that seem specialized for particular reactions are the contractile cells which encircle some of the openings (Fig. 428 A and Fig. 206, p. 308). These cells are called "effectors" and regarded as *independent effectors* comparable with the cnidoblasts of a hydra, which react independently of the hydra's nervous mechanism (*cf.* Fig. 217, p. 326). There seem to be no nerve cells and no sensory cells, although every cell of the sponge has some capacity of reacting to stimuli. The reactions that occur spread slowly in all directions from the point stimulated, apparently as a result of transmission from cell to cell throughout the mass and not of transmission by any special cells that might be called nerve cells. Transmission of this sort is called *neuroid transmission* in contrast to *neural transmission* by means of nerve cells. It seems, therefore, that independent effectors are the only specialized units in the receiving and reacting mechanism of sponges.

In the Cœlenterata, the mechanism is like that described for the hydra (Fig. 428 B and Fig. 217, p. 326). Sensory cells and neuro-sensory cells are the *receptors*; nerve cells have the function of *neural transmission*; and muscle processes of the large ectoderm cells are *effectors*. The processes of the cells composing this system seem to be continuous like a network and not to make contact by synapses (*cf.* p. 326) as do the nerve cells of higher invertebrates and of vertebrates. In addition, the cnidoblasts appear to be *independent effectors*, since they react independently of the nervous mechanism. There is no centralization of nerve cells save for the slight concentrations in rings encircling the base and the hypostome in hydras and more obvious concentrations encircling the margin of the body, as in jellyfishes. In forms having such "nerve rings" there is little indication of anything resembling the adjustment of impulses and consequent reflex action that is characteristic of a central nervous system. In contrast to the neuroid transmission of sponges the transmission of cœlenterates is through nerve cells and hence is called *neural transmission*, although the impulses travel in all directions in the cœlenterate and not to a particular effector as in more specialized systems. The Cœlenterata have, therefore, a *receptor-effector* system in contrast with the Porifera, which have only effectors that are stimulated and that react independently.

In the Annelida the nervous mechanism is representative of that found in all invertebrates that have well-developed nervous systems (Fig. 428 C). Specifically, in the earthworm (Fig. 337, p. 456) neuro-sensory cells in the epidermis are the *receptors*. Each of these cells has a principal process or axon (*cf.* p. 455), extending as a nerve

fiber that enters the ventral nerve cord, and lesser processes of these cells may connect with the nerve cells of a *subepidermal nerve net*. Within the nerve cord the neuro-sensory-cell fibers may have synapses (cf. p. 455), with *efferent neurons*, or their synapses may be with the nerve cells that are called *adjustor neurons* because they seem to

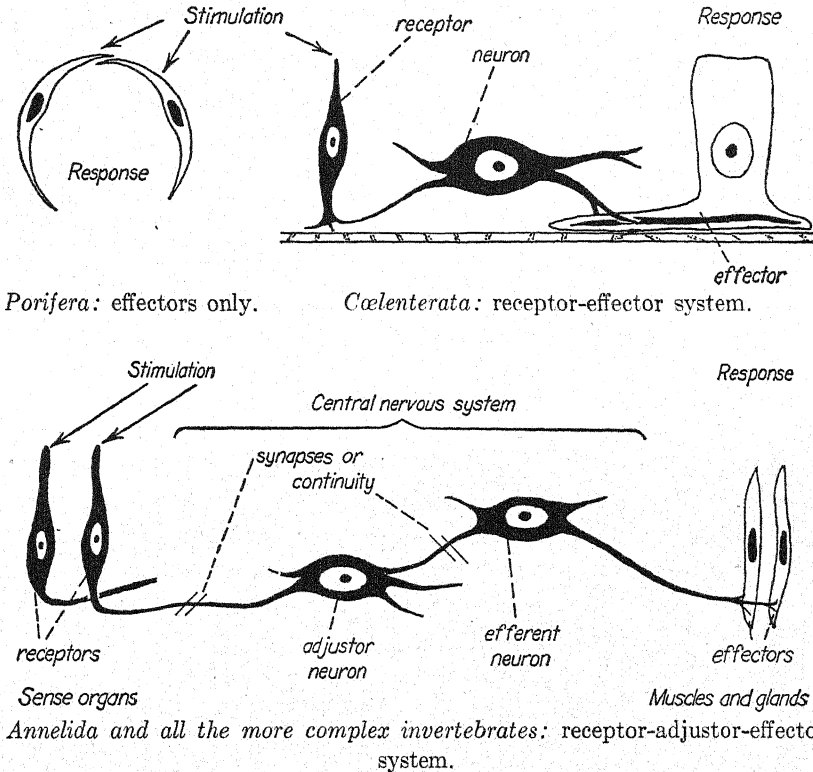


FIG. 428. Invertebrate nervous mechanisms; schematic.

"adjust" incoming to outgoing impulses. Adjustor neurons may be further defined as nerve cells with processes confined to the ventral nerve cord and thus differing from the efferent neurons from which the principal processes or axons (cf. p. 456) extend outward to contacts with the muscle cells or *effectors*. The resemblance of such a cellular mechanism to that found in vertebrates is apparent (cf. Fig. 39, p. 70). The nervous mechanism of the annelid, like that of the vertebrate, consists of a *central system*, the nerve cord and so-called "brain," and a *peripheral system* of nerves which are composed of nerve fibers. Moreover, the worm and the vertebrate have sensory cells and sense organs

which act as receptors and also muscle and gland cells which are the effectors.

In the earthworm the *nerve impulses*, which are set up in the neuro-sensory cells as a result of stimulation, travel to the subepidermal nerve net and also along the axons of the sensory cells that extend into the ventral nerve cord. Within the nerve net the impulses seem to travel in all directions from their point of origin but not for any great distance. Within the nerve cord the pathway may be a short cut to an efferent neuron and thence outward, or it may involve adjustor neurons and so a pathway that can extend to any part of the animal. In addition to such adjustor neurons as those shown in Figure 337, p. 456, there are in the earthworm what are called giant fibers and their related nerve cells, which seem to be a mechanism for long-distance transmission.

Thus the fundamental relationships, as shown by Figure 39, p. 70, and Figure 337, p. 456, are similar in the vertebrate and the annelid. Each nervous system is a *receptor-adjustor-effector mechanism*. The difference between the two systems lies in the degree of complexity and not in the fundamental relationship of parts, particularly the presence of more adjustor neurons and hence more complicated connections within the central nervous system of the vertebrate. The brain of the vertebrate is a region in which the number of adjustor neurons, and consequently the complexity of pathways for nerve impulses, has been greatly increased. The vertebrate brain is also the region that is most intimately connected with the more specialized sense organs. The "brain" and near-by region of the nerve cord of the annelid are likewise connected with the sensitive anterior end of the earthworm and with the sense organs on the head of such an annelid as the clamworm (cf. Fig. 328, p. 444).

When the nervous system of the annelids is compared with that found in coelenterates, the following lines of specialization are apparent (Fig. 428 B and C). In the annelids a central system contains adjustor neurons which are not present in the coelenterate, and nerves connect this system with sense organs and with the musculature. There is also the beginning of a brain region at the anterior end of the central system, in correlation with the development of a head end with special sense organs. Related to this development of a central system is the development of one-way transmission and so of reflex circuits, and of synapses in place of connections through networks of cell processes. But nerve nets are found in the subepidermal region

and elsewhere in the annelid. The other elements of the annelid system are comparable with those of the coelenterate as shown in Figure 428.

In the Mollusca and the Arthropoda the nervous system is a receptor-adjustor-effector mechanism essentially like that of the annelids (Fig. 428 C). Active and highly specialized forms, such as the squids among the Mollusca and many insects and the spiders among the Arthropoda, have specialized sense organs and effectors and hence adjustor mechanisms of greater complexity. But the difference is one of degree, not of kind, since the specialization is still within the framework of a receptor-adjustor-effector system. The same situation exists in connection with the mechanisms of nervous coördination in the vertebrates (Fig. 39, p. 70). Hence from the earthworm to man the difference consists in the increased number and specialization of receptors, adjustors, and effectors, not in changes of the basic cellular mechanism.

Overall comparisons of the nervous systems found in the invertebrate can be made by such generalized diagrams as those shown in Figure 428. The protozoan may be included in these comparisons because the responses of protozoan cells are comparable with those of individual metazoan cells. Moreover, interesting parallels can be noted if the protozoan is compared with the metazoan as an individual reacting to its environment. Such a protozoan as one of the complex ciliates receives stimuli and reacts in characteristic fashion. Sensory cilia can be compared with receptors; there is something like transmission within the cell; and, if there are contractile fibrils, they may be compared with the muscle cells which are effectors in the metazoan. In the sponge there seem to be only effectors, which are called *independent effectors* because they must act independently in the absence of any receptor mechanism and so resemble the independent effectors of more complex animals. A *receptor-effector mechanism* is found in such invertebrates as the coelenterates, and the cells seem to be connected as a network and not by synapses. The turbellarian worms show the beginnings of a central nervous system, consisting of "brain," ventral nerve cords, and "nerves"; and they seem to have adjustor neurons, although the cellular relationships in these worms are hard to determine. In annelid worms it is clear that there are a considerable number of adjustor cells and hence a *receptor-adjustor-effector mechanism*; and there are synapses, although networks are found beneath the epidermis and in the gut wall. The diagram of the vertebrate system (Fig. 39, p. 70) extends the comparison to all the phyla of the Animal Kingdom.

Skeletal Systems

The skeletons of animals have the functions of protection and support, and they may serve for the attachment of muscles, which can thus pull from a firm place of support. They are of two general types, called *exoskeletons* or *endoskeletons* according to their origin at the external surface of the animal or within the deeper parts of its body. Although the great majority of skeletons among invertebrates are exoskeletons, there are examples of what can be properly called endoskeletons, notably the skeletons of echinoderms.

Here again a parallelism exists between the skeletons formed by the Protozoa and the skeletons of Metazoa. In the Protozoa some skeletons are external secretions, and others are formed within the cell body. Thus, *Arcella* secretes an external skeleton, and *Diffugia* an external covering which cements together sand grains and similar foreign particles; in *Trachelomonas* the firm external covering, which arises by differentiation of the cell surface, is essentially an external skeleton (cf. Fig. 154, p. 241). On the other hand, the rodlike bodies related to the locomotor apparatus in some flagellates and formed within the cell seem to function as supporting structures and so resemble internal skeletons.

The skeletons of Porifera are composed of spicules or of fibers or of both spicules and fibers. Since these spicules and fibers originate from cells within the middle layer of the sponge, and even as bodies within the cytoplasm of the cells that form them, the sponges have an internal skeleton (cf. Fig. 202, p. 305). Many Cœlenterata have no skeletons, except as the supporting lamella of a hydra functions as an elastic membrane to which cells and muscle processes are attached, or the mesoglea of a jellyfish functions as a blubberlike mass that supports the softer parts. In hydroids the stems of the colony may be encased in a cuticular exoskeleton secreted by the ectoderm (Fig. 221, p. 332), and the calcareous skeletons of corals are likewise formed as ectodermal secretions. The cœlenterates called "sea-pens" and "sea-fans" have internal skeletons of spicules secreted by cells within the mesoglea, although these cells have reached the mesoglea by migration from the ectoderm. Many representatives of the lesser phyla have cuticular exoskeletons (cf. Bryozoa, Fig. 287, p. 400); others, calcareous exoskeletons or shells (cf. Brachiopoda, Fig. 291, p. 405).

The Mollusca have only exoskeletons in the form of shells secreted by the ectoderm of the dorsal body surface. This molluscan skeleton is always a one-piece structure in the embryo or larva. Its division

into right and left parts, as in the clams and mussels, or into a series of parts, as in the chiton (Fig. 317, p. 430), is secondary. The seemingly internal skeleton, or "pen," of the squid originates in the embryo as a secretion from a part of the dorsal ectoderm that sinks into the interior as the development proceeds. Typically, the exoskeletons of mollusks provide for indefinite growth by additions at the margin and by a limited thickening.

The Arthropoda have exoskeletons of chitin secreted by the ectoderm and, in such forms as the crayfishes, lobsters, and crabs, strengthened by carbonate of lime. Internally, there may be muscle tendons stiffened by chitinous and limy deposits. A unique feature of the arthropod skeleton is its periodic molting. As a result the increase in size is commonly restricted to a short period just after the molt, because the chitinous skeleton does not stretch or otherwise grow once it has "set."

Echinoderms such as the sea-urchins may seem to have an external skeleton, but in reality the skeleton of the sea-urchin and of other echinoderms is mesodermal in origin and therefore an endoskeleton. In the starfish this skeleton is for the most part still internal, although covered by only a thin layer of tissue. The holothurians (*cf.* p. 555) may have skeletons composed of easily recognizable plates, or the plates may be reduced to microscopic remnants. In all cases the echinoderm skeleton consists of separate plates formed in the mesoderm. The independence of the close-fitting plates in the starfish, the sea-urchin, and the sea-lily can be demonstrated by boiling in caustic potash, after which the plates fall apart like the disarticulated skeleton of a vertebrate.

Reproductive Systems

The reproductive organs of invertebrates show only general similarities of structure when comparisons are made among the animals in different phyla; within any phylum they are, of course, homologous. But similarities in the functions of parts which are in no wise homologous are frequently observed, for example, in the parts that secrete protective membranes for the eggs in various phyla, or in the seminal receptacles where spermatozoa are retained for subsequent fertilization of ova.

The Mesozoa and Porifera have nothing that can be called reproductive organs, only reproductive cells (Fig. 429 A). The Coelenterata (Fig. 429 B and C) and other forms, such as the Ctenophora, have localizations of the germ cells called *ovaries* and *testes* but nothing that

can be called a system in the sense of a group of structurally related organs performing some general function. In Platyhelminthes the reproductive organs have a surprising complexity and a high degree of uniformity throughout the phylum, although found in simplified form in some turbellarians. In Nemertinea (Fig. 430 A) the reproductive organs are simple pouches, each ovary or testis a sac with its own external opening. The contrast between the reproductive organs

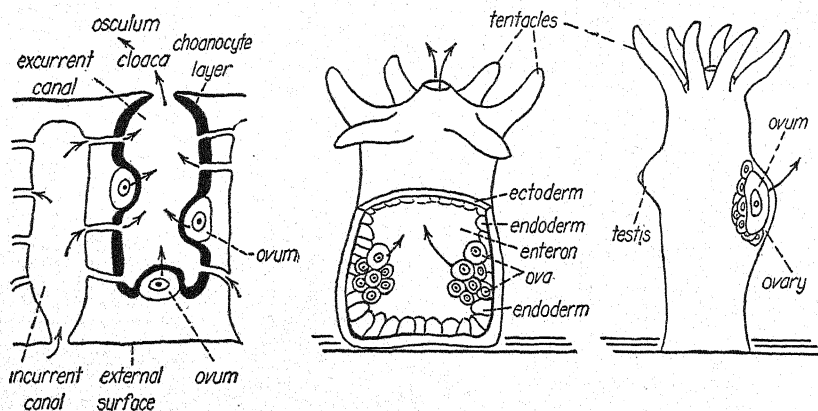
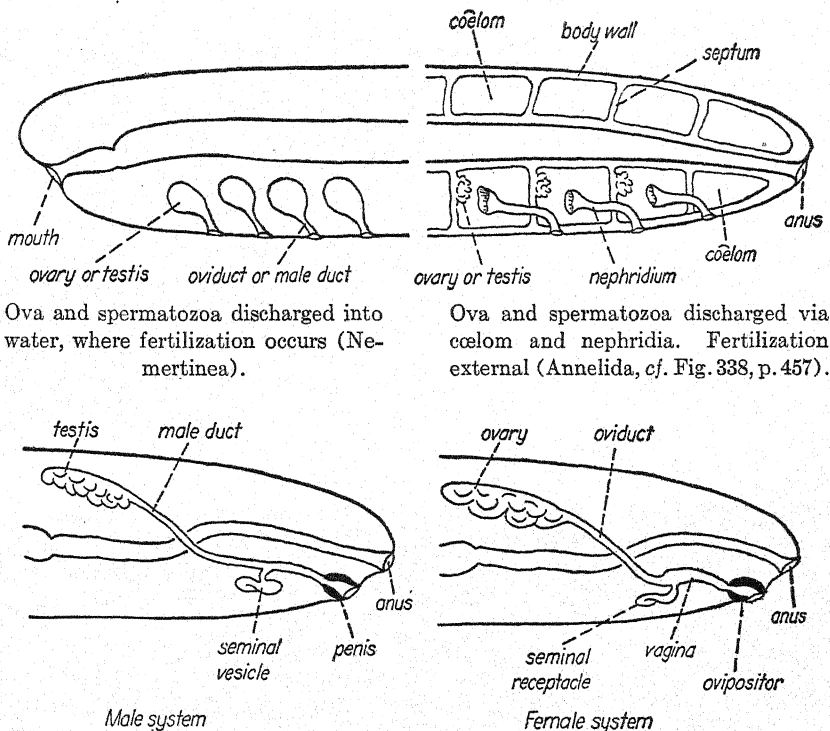


FIG. 429. Reproductive systems in some of the simplest invertebrates; schematic. *Left*, the ova and spermatozoa arise from cells of the middle region. The ova are fertilized in place and develop into ciliated larvæ, which break through the choanocyte layer into the excurrent canals and are discharged via the cloaca and osculum (Porifera, cf. Fig. 201, p. 304). *Middle*, the ova and spermatozoa arise from endoderm cells, are discharged into the enteron, and thence through the mouth (Scyphozoa and Anthozoa, cf. Fig. 225, p. 336). *Right*, the ova and spermatozoa arise from the ectoderm and are discharged into the surrounding water (Hydrozoa, cf. Fig. 220, p. 331).

of a platyhelminth and a nemertinean well illustrates the dissimilarities of these organs among the phyla of invertebrates.

Referring to other representative examples, we find that the male and female systems of the nematode *Ascaris* (Fig. 272, p. 385) present a moderate degree of complexity. In the pelecypod Mollusca, such as the fresh-water mussel (Fig. 298, p. 415), the ovaries and testes are saclike structures producing the ova or spermatozoa from their epithelial linings and having ducts with no special functions except discharge of the sex cells (cf. Fig. 430 A). The only complications in the pelecypods consist of the brood-pouches of various sorts, such as the modified gills of the fresh-water mussels (Fig. 302, p. 420), in which the eggs of some species begin their development. In the gastropod

and cephalopod Mollusca the reproductive ducts are variously modified to produce gelatinous secretions that surround the fertilized eggs and to facilitate the sexual union and egg-laying. In the Annelida (Fig. 430 B) such forms as the clamworm (Fig. 327, p. 443) produce the ova



Ova and spermatozoa discharged into water, where fertilization occurs (Nemertinea).

Ova and spermatozoa discharged via coelom and nephridia. Fertilization external (Annelida, cf. Fig. 338, p. 457).

Ovaries and testes not obviously related to a coelom. Seminal vesicle, seminal receptacle, penis, and ovipositor related to sexual union and egg-laying (Insecta, cf. Fig. 360, p. 490).

FIG. 430. Reproductive systems in some of the more complex invertebrates; schematic.

and spermatozoa from peritoneal cells lining the coelom and discharge them through the nephridia, whereas such forms as the earthworm (Fig. 338, p. 457) have reproductive organs so complicated that they seem entirely unlike those in the clamworm. Careful study, however, reveals the essential features, the ovaries, testes, and their ducts, to be similar in these two types of annelid.

The earthworm with its localized testes and ovaries, its seminal vesicles and specialized male ducts, and its oviducts with egg-sacs,

is an example of a complicated system that has probably been evolved within one subdivision of the Phylum Annelida from a simpler organization like that of the clamworm. The earthworm's system is further complicated by the presence of accessory parts, the clitellum, the seminal receptacles, and certain skin glands related to the sexual union and egg-laying, which are not directly connected with the reproductive organs, but which play important parts in the reproductive process.

The reproductive organs of Arthropoda (*cf.* Fig. 430 C) exhibit great variety in correlation with the diversified structure and activities of the members of this phylum. In the locust (Figs. 360 and 369, pp. 490 and 500) the female system consists of ovaries, oviducts, seminal receptacle, vagina, and ovipositor; and the male system consists of testes, ductus deferentia, accessory glands, ejaculatory duct, and penis. In Echinodermata the reproductive organs consist, typically, of five saclike organs, each with its own opening in an interradiar position (*cf.* Fig. 412, p. 549). From these organs the ova or spermatozoa are discharged into the sea water, where fertilization and development occur in the great majority of echinoderms. The only exceptions are a few species in which the fertilized eggs begin their development within some form of brood-pouch.

The diversity in the structure of invertebrate reproductive systems is sufficiently illustrated by the foregoing review. Obviously, there is little similarity beyond the presence of ovaries, testes, and their respective ducts, although it is possible to make comprehensive diagrams (*cf.* Figs. 429 and 430). Further complications of these systems are related to the reproductive habits and modes of development in the many types of invertebrates. When these systems are compared for the functions of their parts, it is seen that similar functions have been assumed in many different instances by structures that are not homologous. Hence, many different kinds of reproductive systems have arisen independently in the evolution of invertebrates. What has happened in this evolution is that various invertebrates have solved their problems of reproduction in ways that are comparable, although effected by different structures.

If we summarize all these facts on a functional rather than a structural basis, there must be first of all sex cells, produced in gonads and discharged to the outside by what may be termed the gonoducts (nemertinean, fresh-water mussel, echinoderm). There may be an eggshell or capsule that protects the egg or embryo (planarian, earthworm, crayfish) and that is produced in various ways. In most of the Eucelomata (*cf.* Fig. 135, p. 215), the germ cells are discharged from

the gonads into the coelom and pass to the outside either through the nephridia (clamworm) or through gonoducts that in many animals seem to have been evolved from nephridia.

Other complications are related to the reproductive habits. For example, fertilization and development may occur in the open water or in a brood-pouch. Fertilization may be assured by simultaneous discharge of ova and spermatozoa or by some form of sexual union. If sexual union occurs, there may be seminal vesicles, in which the sperm cells are retained temporarily in the male, and seminal receptacles, in which the sperm cells received during sexual union are retained by the female until fertilization (earthworm). There may be a copulatory organ such as the penis (planarian and locust), and there may be an ovipositor to aid in the egg-laying (locust). If development occurs within the female gonoducts, in contrast to development in a brood-pouch which, strictly speaking, is not a part of the reproductive system, the female duct may be modified accordingly. Thus, some invertebrates can be called *ovoviviparous* for the same reason that some vertebrates are so called (*cf.* p. 128). In all these examples the functions are similar, but the parts involved are as diversified as the many kinds of invertebrate reproductive systems. It appears that in the course of evolution different invertebrate types have arrived independently at similar solutions to the problem of safer and more effective reproduction.

Thus, there are many functional comparisons or analogies among the reproductive systems of invertebrates, but only very general structural resemblances or homologies. One of the most general of these structural resemblances is the complex formed by the gonads, the coelom, the nephridia, and the gonoducts in the Eucœlomata (*cf.* Fig. 135, p. 215), as shown by Figure 427 D, a resemblance which many zoölogists believe to be indicative of evolutionary relationships.

Summary

In conclusion, it is evident that the basic problems of metabolism, irritability, and reproduction have been solved by animals in a variety of ways. In such a function as excretion the organs are remarkably similar in many of the phyla. The cellular mechanism of the nervous system shows marked similarities in all the more complex animals; and the simpler mechanism represented in the coelenterates can be compared, so far as it goes, with those found in higher animals. Comparing the mechanisms of response from the sponge to man suggests, as the broad steps in the evolutionary origin of the animal

nervous system, an evolution from effectors only, to a receptor-effector system, and then to a receptor-adjustor-effector system of increasing complexity. On the other hand, respiratory systems show the greatest diversity of structure, although the basic relationship is always the same, namely, an arrangement in which the blood or body fluids of the animal are separated from an external source of oxygen by a thin layer of cells through which the gas can be diffused. The structure of reproductive systems may not be homologous, and yet the same functions may appear in widely different systems. Skeletons are of many different sorts, although they may be classified as external or internal. Taken all together, the organ-systems make up the anatomy of the animal, which is the basis for comparisons among the various phyla. One of the things that must strike anyone who first examines the many forms of invertebrate life is their endless diversity. It seems at first as though there must be hundreds of different structural types. As the examination proceeds, it becomes more and more apparent that there are relatively few structural types—the so-called phyla. And when the phyla are compared, there are certain broad resemblances. There is, in fact, a surprising degree of unity in the structure of animals despite their seeming diversity.

CHAPTER 19

THE CHORDATA

The Chordata are bilateral, triploblastic animals with a well-developed coelom, except in some of the lower representatives of the group, and with certain structures that are metameric. Chordates are further characterized by a dorsal, tubular, central nervous system, the presence of gill slits at some stage of development, and a primary endoskeleton consisting of an axial rod, the notochord, from which the name of the phylum is derived. In the Division *Acraniata*, which includes the chordates without skulls and without vertebræ, the notochord is the only skeleton whether or not it persists in the adult. In the Division *Craniata* or *Vertebrata*, which includes the chordates with skulls and with vertebræ, the notochord appears in early development but is replaced more or less completely by the vertebræ, which are formed around it when the familiar cartilaginous or bony skeleton differentiates. These two divisions are subdivided as shown in the review of this great animal group which is given on pages 584 and 585.

The chordates are the most widely distributed group of animals. They are found in the ocean at all depths, and on land from rain forest to desert habitats and from the tropics even to the polar regions, where representatives of the warm-blooded mammals and birds occur. They range from species of minute size to the whales, which are the largest of existing animals. Only the arthropods can be compared with the chordates in diversity of habitat and structure. The distribution of arthropods on the land surface is limited, however, because they cannot remain active at low temperatures; and large arthropods, such as the lobsters and some of the crabs, are pigmies when compared with the largest chordates. Although the chordates are not represented in the Cambrian fossils (*cf.* Fig. 469, p. 646), it seems probable that animals of this type, lacking skeletal parts that could be preserved, existed in Cambrian times, since numerous fossils are found in the Silurian, and what are regarded as chordate scales occur in the Ordovician. From the Devonian onward, the fossil record of the Chordata is more comprehensive than that of any other phylum. To study the

evolutionary history and present state of this phylum is to study the remote history and state of the human species, since man is a chordate.

In preceding chapters the frog has been used so extensively to illustrate the principles of structure and function that we shall now consider in detail only the chordates that are not vertebrates. For the vertebrates this chapter undertakes a survey of the principal types and of their evolutionary history. In considering this history we shall be anticipating the subject matter of the next chapter. However, there have been references in previous chapters to the history of animals as an evolutionary process. If we speak of ancestors and descendants as indicated from fossils, it will be on the assumption that the evolutionary interpretation is to be accepted as the most reasonable explanation of the facts. The specific evidence for evolution in general and further examples of the evolution of vertebrates follow in Chapter 20. In view of the references to geologic time and to the fossil record, it is important before proceeding that Figure 438 and also Figure 469, p. 646, be studied carefully and kept in mind. It is also important that the characteristics of the principal subdivisions of the phylum be noted as shown by the classification that follows.

PHYLUM CHORDATA

DIVISION ACRANIATA

Without a skull, or cranium, and without vertebræ and appendages.

Subphylum Hemichordata

Wormlike animals with a notochord in the anterior end of the body, persistent gill slits, and a dorsal nerve cord in addition to a ventral one. *Dolichoglossus* (*Balanoglossus*), etc. (Fig. 431).

Subphylum Urochordata or Tunicata

Adults hardly recognizable as chordates. Larvæ, known as "tadpoles," with a notochord in the tail, gill slits, and a dorsal, tubular, central nervous system. During metamorphosis the notochord is lost, the gill slits are modified, and the nerve cord is reduced to a ganglion. Tunicates, or sea-squirts, etc. (Figs. 432-435).

Subphylum Cephalochordata

With some resemblance to the tadpoles of tunicates and also to fishes, with persistent notochord and gill slits, with a dorsal, tubular, nerve cord but without a skull and vertebræ. The amphioxus, or lancelet, *Branchiostoma* (*Amphioxus*), etc. (Fig. 436).

DIVISION CRANIATA

With a skull, or cranium, and mostly with vertebræ and paired appendages.

Subphylum Vertebrata

Identical with Craniata, since only subphylum in this division.

SUPERCLASS Pisces

With gills and with appendages, usually represented by two pairs of fins typically suited for locomotion in water. The various types of fishes.

Class *Agnatha*

Without true jaws and without limbs. Extinct forms, a large group of primitive fishes armored with large scales, the ostracoderms. Existing forms, without such scales, the lampreys and hags (Fig. 439).

Class *Placodermi*

Armored fishes of specialized type, extinct and not closely related to any existing forms (Fig. 438).

Class *Chondrichthyes*

Sharklike fishes, with exposed gill slits, extinct forms with bony skeletons, existing forms with cartilaginous skeletons (Fig. 440).

Class *Osteichthyes*

With bony skeletons and with gill slits covered by an operculum, including the extinct lobe-finned fishes, the numerous existing ray-finned fishes and the lungfishes.

Common fresh-water and marine fishes (Figs. 441-444).

SUPERCLASS Tetrapoda

With lungs and with appendages, usually represented by two pairs of limbs typically suited for locomotion on land. The air-breathing vertebrates.

Class *Amphibia*

Semiterrestrial and aquatic forms, skin usually soft and moist, cold-blooded, respiration usually by gills in the larvæ and by lungs in the adult, typically with eggs laid and developing in water. Salamanders, frogs, toads, etc. (Figs. 446-451).

Class *Reptilia*

Terrestrial or secondarily aquatic forms, covered with scales or horny plates, cold-blooded, lung-breathing, typically oviparous, some ovoviviparous. Turtles, lizards, snakes, alligators, etc. (Figs. 453-458).

Class *Aves*

Terrestrial forms, adapted for flight, covered with feathers, warm-blooded, lung-breathing, oviparous. Birds (Figs. 459-461).

Class *Mammalia*

Terrestrial or secondarily aquatic forms, covered with hair, warm-blooded, lung-breathing, with mammary glands, mostly viviparous. Mammals (Figs. 462-468).

The Acraniata

The Hemichordata. To the Subphylum *Hemichordata* belong the Classes *Enteropneusta* and *Pterobranchia*. These marine animals have been regarded as chordates because they have gill slits, a notochord, and a nervous system which lies partly in the dorsal position characteristic for the Chordata. Some zoölogists, who are not impressed by the resemblances of the hemichordates to the chordate type of organization, prefer to classify these animals as a separate phylum.

The Enteropneusta. Dolichoglossus (Balanoglossus). The species of this genus and the few related genera, which constitute the Enteropneusta, are marine, wormlike animals that usually live in shallow water and are found burrowing in muddy or sandy bottoms (Fig. 431). A gelatinous mucus, which is secreted by the outer surface of the body and to which sand grains and similar particles adhere, produces a tubular covering as in some of the annelids. Externally, the body shows its division into three regions, the *proboscis*, *collar*, and *trunk*. The *mouth* is located ventrally beneath the proboscis and just within the collar; the *anus* is located at the posterior end of the body. The *gill slits* are openings arranged in a row on each side in the dorsal region and extending for some distance along the trunk posterior to the collar. A lateral ridge ventral to each row of gill slits marks the position of the gonads. Near the middle of the trunk region transverse ridges are formed by paired glandular cæca, which arise from the digestive tract. As the proboscis is forced through the mud or sand in burrowing, the silt from which the food is extracted enters the mouth. The excess water, entering with the food, serves in respiration by passing through the gill slits which lead from the anterior region of the digestive tract. Internally, the *digestive tract* includes a buccal region within the collar, a pharyngeal region with the gill slits, and an intestine with cæca along its middle portion. Cavities called *cæloms* are found within the proboscis, the collar, and the trunk. The *circulatory system* consists of a median dorsal vessel, connected with a median ventral vessel by fine lateral branches in the region of the gill slits and posteriorly; there is a so-called heart, and circulation is by peristaltic contractions of the larger vessels. A supposedly *excretory area* is connected with blood vessels in the proboscis. The *nervous system* is composed of nerve cords, formed as thickenings of the ectoderm in the median dorsal and the median ventral regions and connected anteriorly by a ringlike thickening of ectoderm beneath the collar. A structure supposedly comparable with a *notochord* is found within the posterior

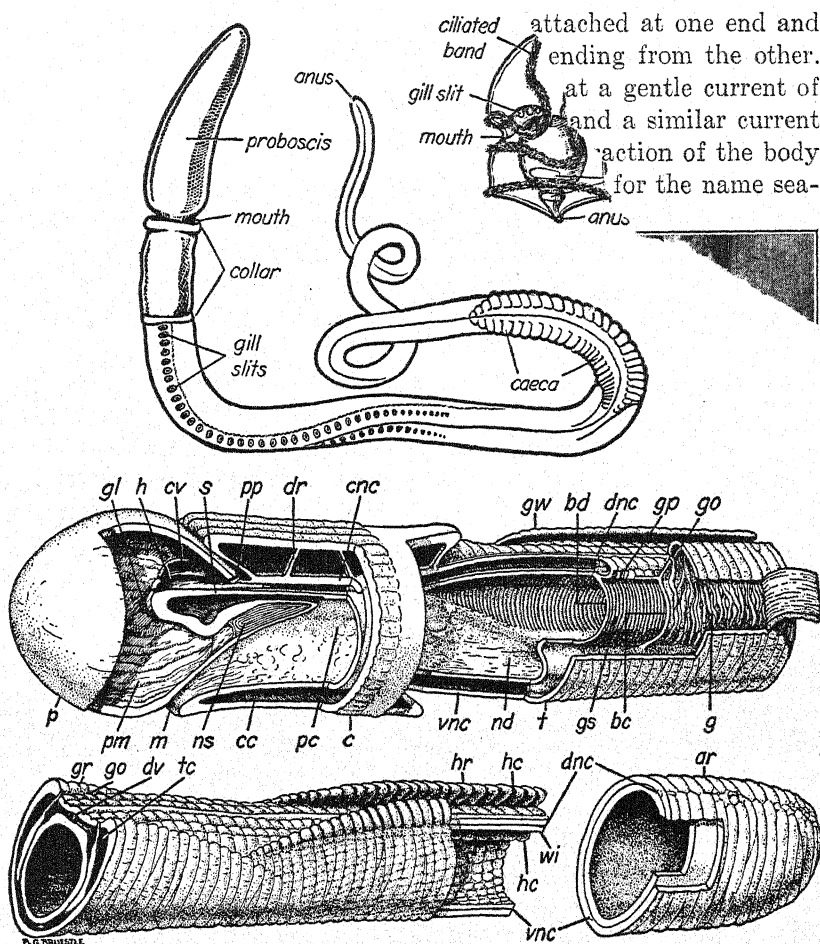


FIG. 431. *Dolichoglossus* (*Balanoglossus*), one of the Hemichordata. Above, external features of the adult, and the larval stage called the *tornaria*. Below, internal structure. *ar*, abdominal region; *bc*, branchial chamber; *bd*, upper portion of pharynx; *c*, collar; *cc*, coelom of collar; *cnc*, collar nerve-cord; *cv*, cardiac vesicle; *dnc*, dorsal nerve-cord; *dr*, dorsal root; *dv*, dorsal vessel; *g*, gonads; *gl*, glomerulus; *go*, genital opening; *gp*, gill-pore; *gr*, genital ridge; *gs*, gill slit; *gw*, genital wing (pleura or ala); *h*, heart; *hc*, hepatic cæcum; *hr*, hepatic region; *nd*, ventral portion of pharynx; *ns*, nuchal skeleton; *p*, proboscis; *pc*, perihæmal coelomic pouch of trunk coelom; *pm*, proboscis musculature; *pp*, proboscis pore (a coelomoduct); *s*, stomochord ("notochord") with cavity opening into buccal cavity; *t*, trunk; *tc*, coelom of trunk; *vnc*, ventral nerve-cord; *wi*, wall of intestine.

(Below, from T. H. Bullock, 1945, *Quarterly Journal of Microscopical Science*, vol. 86.)

The sexes are separate, and the gonads are sacculated serially on each side in the region of the notochord. The notochord is projected to the outside by pores when mature. The Classes *Enteropneusta* and *Hemichordata*. Fertilization takes place externally. A pelagic larva has been regarded as characteristic for the *Enteropneusta* (Fig. 431), is enough like the dipleurula larva of *Ascidacea* and a nervous system (Fig. 431), is enough like the dipleurula larva of *Ascidacea* (Fig. 431) to suggest a remote evolutionary connection between the *Enteropneusta* and hemichordates. On the other hand, the resemblance between the notochord, the gill slits, and the dorsal portion of the nervous system are the basis for classifying the *Enteropneusta* as Chordata.

The Pterobranchia. Cephalodiscus and Rhabdopleura. These small marine forms have the body divided into *proboscis*, *collar*, and *trunk* regions and have an internal structure comparable with that of *Dolichoglossus*. In correlation with their attached mode of life and their association as groups of individuals secreting a common covering, the trunk region is U-shaped, so that the *anus* opens near the *mouth* at the distal end of the attached individual. Not much is known regarding their development, since they occur in fairly deep water and have been collected in relatively few localities, although these localities are scattered over both hemispheres.

The Urochordata or Tunicata. In the Subphylum *Urochordata* are included the Classes *Ascidacea*, *Larvacea*, and *Thaliacea*, all of which are marine animals. Of these, the *Ascidacea*, or "sea-squirts," are the most commonly known; the *Larvacea* are a problematical type; the *Thaliacea* are the most specialized.

The Ascidacea. The important features of the *Ascidacea* are their specializations for an attached mode of life and their apparent evolution from free-living ancestors. The *Ascidacea* were long classified as mollusks, their true relationships being recognized only when the developmental stages became known in 1866. It was then apparent that the resemblances to mollusks were superficial and that the early stages of development showed clearly the chordate nature of the *Urochordata*. Indeed, this example of the establishment of relationship through knowledge of developmental stages is one of the most celebrated in the history of embryology.

The sea-squirt, *Molgula manhattensis*, is one of the species of tunicates most abundant upon the Atlantic Coast of North America. Although *Molgula* is found attached to various submerged objects in shallow water, it is most easily collected from the piling under harbor wharves, where it is often abundant along with other ascidians, such as *Styela partita* and *Ciona sociabilis* (Fig. 432). Like *Ciona*, an ex-

panded *Molgula* appears as a globular mass attached at one end and having two tubular processes, the *siphons*, extending from the other. If the animal is not disturbed, it can be seen that a gentle current of water is flowing into the longer of these siphons and a similar current outward from the shorter one. The fact that contraction of the body drives a jet of water from each siphon is the reason for the name sea-squirt. From the water entering the incurrent siphon the animal obtains its food, by straining out the minute organisms, and its oxygen for aerating the blood. Since the feces and reproductive products are discharged from the excurrent siphon, along with outflowing water, the relationships are superficially like those of a pelecypod mollusk (cf. p. 415).

The following account of the *internal structure* and functions is sufficiently general for the various species that are commonly studied. The entire body is covered by a thick membrane, the *test* or *tunic*, which is firmly attached only in the region of the two siphons and which can be removed without disturbing the essential parts of the animal (Fig. 433). The test, in fact, functions as a tough, elastic shell, although it contains the cells by which it is formed and blood spaces through which nutrient material reaches these cells. The material giving the test its toughness is closely similar to, if not identical with, cellulose, which is a compound rarely produced by animal tissues. The true outer, or ectodermal, surface of the body is exposed only by the removal of the test. Most of this surface is the so-called *mantle*, which encloses an extensive cavity called the *atrium*. The excurrent siphon is essentially a specialization of the mantle enclosing the median portion of the atrial cavity, from which lateral portions extend on each side beneath the mantle. Since the atrium is formed as an invagination of the outer surface, it is lined with ectodermal cells, and the mantle consists of an inner and outer ectodermal layer with an intervening region of muscle fibers, connective tissue, and blood sinuses. To understand the processes involved in feeding and respiration it is neces-

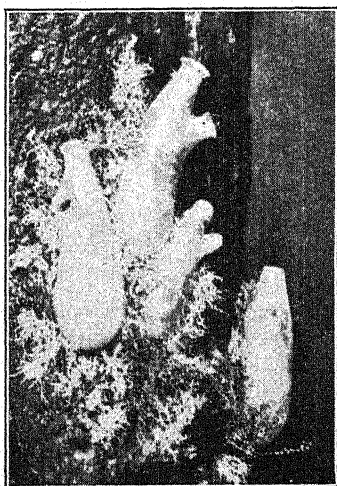


FIG. 432. A simple tunicate: four individuals of *Ciona sociabilis*, attached to a wharf pile.

(From W. G. Van Name, 1925, *Natural History*, vol. 25; courtesy of American Museum of Natural History.)

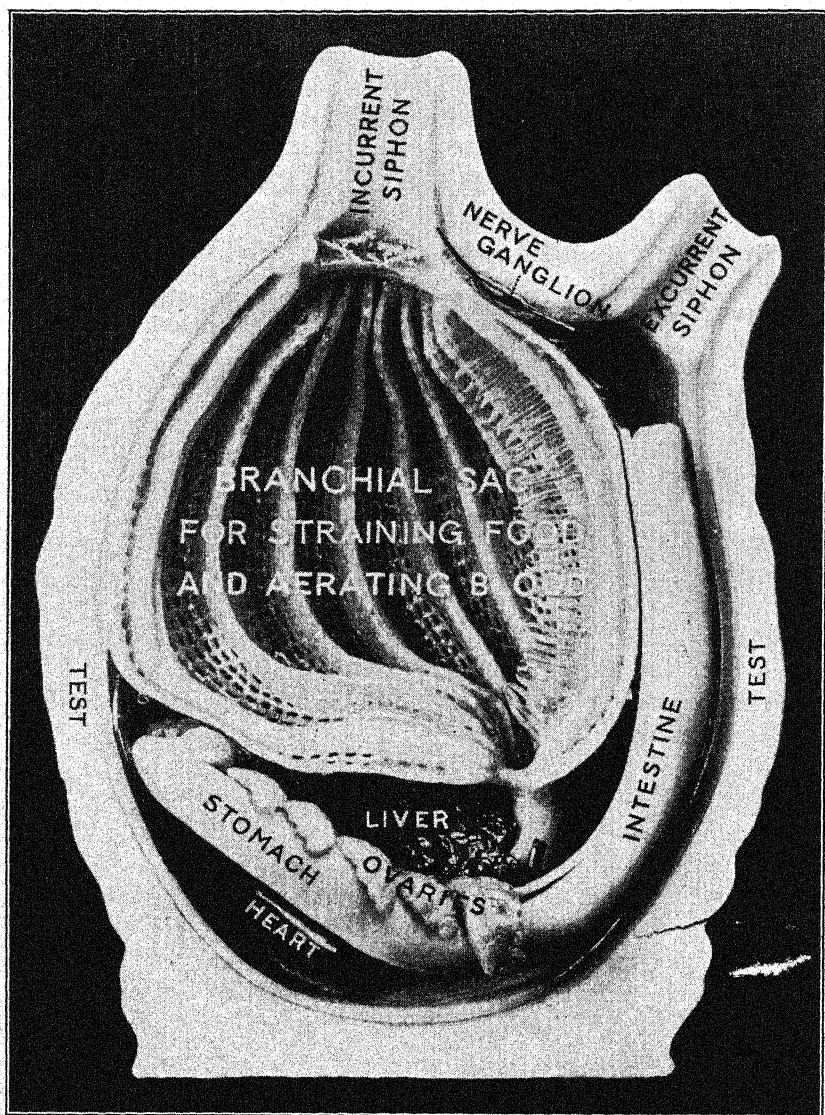


FIG. 433. Internal structure of a tunicate; photograph of a model.
(From W. G. Van Name, *op. cit.*; courtesy of American Museum of Natural History.)

sary to understand the structural relationships of the *digestive tract* and atrium. The opening of the incurrent siphon may be called the mouth, and the cavity within this siphon the oral cavity. A circlet of tentacles marks the beginning of the pharynx, or branchial sac, which is relatively large and specialized for food-collection and respiration. The relationships of the siphons, pharynx, esophagus, stomach, intestine, and anal opening are apparent from Figure 433. A digestive gland, sometimes called the liver, is connected with the stomach by a duct. Water passes into the mouth, enters the branchial sac, and passes through the many small openings in its wall into the atrial cavity on either side and thence to the excurrent siphon, from which it is discharged. The openings in the branchial sac thus function in the manner of the less numerous openings called gill slits in other chordates. As in the Hemichordata, food is obtained by straining the nutrient material from water received through the mouth and discharged through lateral openings in the pharynx. In the tunicate the food particles, consisting of minute organisms, are caught in mucus as the water leaves the pharynx and conveyed by cilia along a definite path to the esophagus, while the oxygen dissolved in this water diffuses into the blood within the vessels of the pharynx.

The *circulatory system* consists of a tubular heart, lying along the outer curvature of the stomach (Fig. 433), with vessels extending from one end directly to the pharynx and mantle and from the other end to the stomach and near-by organs, and thence to the pharynx. A unique feature is the reversal of the heart beat. After the peristaltic contractions have been passing in one direction for a short time, the beats cease and are then resumed in the reverse direction with a corresponding reversal of the blood flow. There are no true blood vessels, only extensive tubular cavities without an endothelial lining. There is no cavity that can be called a coelom, unless the pericardium and the cavities within the excretory and reproductive organs can be so designated. A mass of tissue, without a duct and lying near the intestine, is presumed to be excretory in function, since it contains uric acid. The *nervous system* consists of a single elongated ganglion, embedded in the mantle between the two siphons, and of nerves extending from each end of this ganglion to the siphons and other parts of the body. A glandular mass beneath the ganglion has been compared to the hypophysis of vertebrates.

Most tunicates are hermaphroditic. The *reproductive organs* consist of an ovary and a testis, lying against the intestine, with ducts opening into the atrial cavity near the anus (Fig. 433). In most of

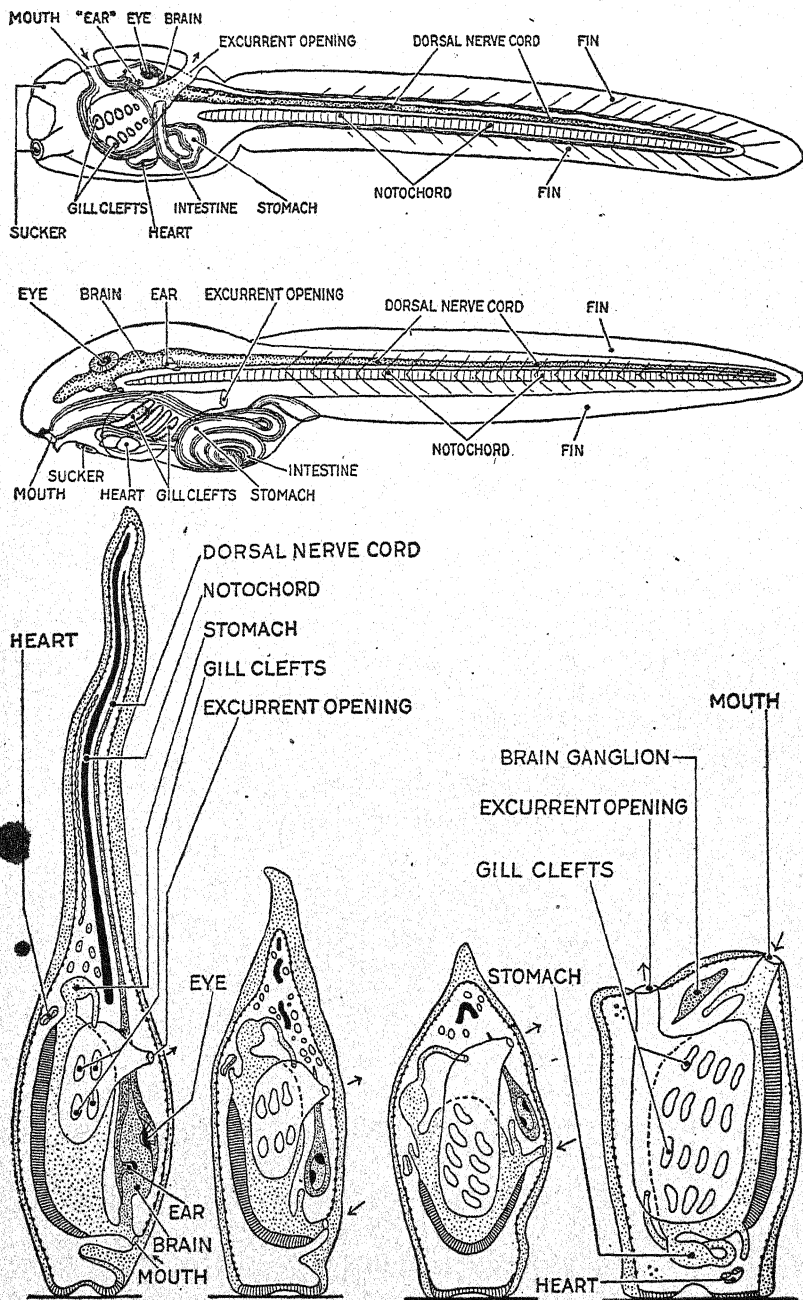


FIG. 434. Tadpoles of tunicate and frog, and metamorphosis of the tunicate tadpole. Above, tunicate tadpole. Middle, frog tadpole. Below, attachment and metamorphosis of tunicate tadpole.

(From W. G. Van Name, *op. cit.*; courtesy of American Museum of Natural History.)

the non-colonial ascidians, such as *Molgula*, the gametes are discharged into the atrium and fertilization takes place in this cavity or in the external water, where the development occurs. The cleavage, blastula, gastrula, and neural-fold stages are comparable with those of the

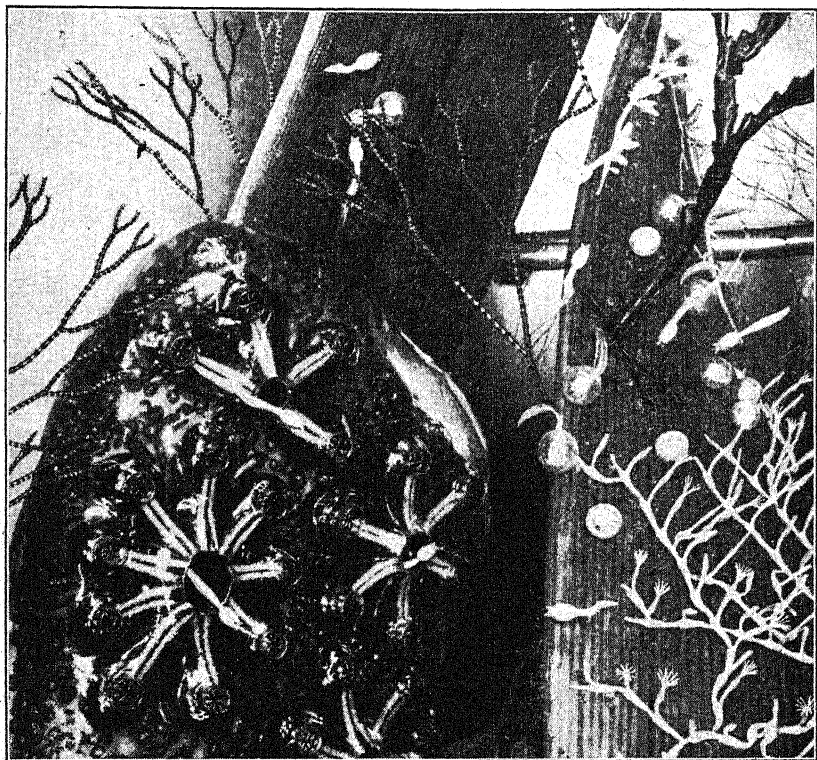


FIG. 435. The compound tunicate, *Botryllus gouldii*, attached to eel-grass. Larvæ are shown issuing from the common excurrent openings and upon the eel-grass.

(From Roy W. Miner, 1925, *Natural History*, vol. 25; courtesy of the author and of the American Museum of Natural History.)

amphioxus (Fig. 81, p. 138). The larva, which is called a *tadpole*, possesses a dorsal, tubular nervous system, a notochord, and gill slits (Figs. 434 and 435). Later this larva becomes attached by suckers at its anterior end and undergoes a complicated metamorphosis during which its chordate features, with the exception of the gill slits, are lost. The gill slits are modified to form the many openings of the adult pharynx. This mode of development is most reasonably explained by the assumption that tunicates have descended from chordate ancestors

that were not attached but free living. Upon such an assumption the tunicates are classified as a subdivision of the Chordata.

In contrast with the simple ascidians, such as *Molgula* and *Ciona*, the so-called compound ascidians are forms in which budding has produced colonies of various sorts. Thus, in *Botryllus gouldii* (Fig. 435) colonies are formed consisting of several individuals, each with its own incurrent opening but with a common excurrent opening near the center of the mass. In *Amarœcium* large masses are formed having a common tunic and consisting of many groups of individuals around excurrent openings, as in *Botryllus*. In *Perophora viridis* root-like extensions, or stolons, extend over a surface and give rise to additional individuals by budding. In most compound ascidians the eggs are fertilized and development proceeds within the atrium as far as the tadpole stage; the larvæ are then discharged through the atrial opening (Fig. 435).

The Larvacea and Thaliacea. The *Larvacea*, which include only a few species of peculiar structure, are more like the tadpoles than the adults of other ascidians. Whether they are a primitive or a degenerate type is problematical. The best-known genus is *Appendicularia*. The *Thaliacea* include a wide range of forms, mostly unattached and with some powers of locomotion but typically borne along by the currents of the ocean. They are clearly tunicates, although greatly modified. Their anatomy and development indicate that they have evolved from ancestors that were attached like the ascidians of today. If this is true, they are animals that were originally unattached, as the ascidians are supposed to have been, then became attached, and subsequently became detached and acquired related modifications. Budding is extensively developed in some of these forms, and thus asexual generations alternate with sexual ones. In some species development occurs within the parent, and the embryo is attached by a placentalike structure and nourished by diffusion from the parent's blood. Familiar genera are *Salpa* and *Doliolum*.

The Cephalochordata. The Subphylum *Cephalochordata* includes only the Class *Amphioxii*, a small group of marine animals, long regarded as closely related to the Vertebrata. It now appears that the cephalochordates are not thus allied to vertebrates. They seem more closely related to the tunicates than to any other subdivision of the chordates. Perhaps they represent an early offshoot from the tunicate ancestry that gave up the attached mode of life, became again free-living animals, and so in the long course of evolution reached their present state.

The Amphioxii. Branchiostoma lanceolatum. The best-known species among the few genera that compose the Class *Amphioxii* is *Branchiostoma (Amphioxus) lanceolatum*, which occurs in European waters (Fig. 436). The common name for this species is the "lancelet," but the original generic name "Amphioxus" has come to be the common scientific designation. The animals are found in shallow water, buried in the bottom with the anterior end protruding, at rest on the bottom, or swimming freely. They usually swim, and also bury themselves tail foremost. The Genus *Amphioxides* is apparently pelagic in its adult stage. In *amphioxus* the body is elongated and compressed laterally. A median *dorsal fin* that extends the length of the body and a shorter *ventral fin* are specialized posteriorly as a more conspicuous *tail-fin*. Anterior to the ventral fin two keel-like ridges, which mark the position of the gonads, extend along the ventro-lateral regions. The *mouth* is located anteriorly within a hoodlike structure, the edge of which is surrounded by a fringe of delicate processes called *cirri*. The *anus* is located on the left side near the base of the tail fin. Another opening, the *atriopore*, by which the water that has passed through the mouth and gill slits finds exit, is located just anterior to the ventral fin. The metameric arrangement of the musculature is conspicuous as seen through the thin ectodermal covering of the animal in the same manner as the muscle segments in the tail of a frog tadpole (Fig. 450 G).

The *digestive tract* consists of a pharynx, or branchial sac, perforated by gill slits, and an intestine leading to the anus. A saclike digestive gland, called the liver, is attached to the anterior end of the intestine. Within the body and surrounding the pharynx, except dorsally, is a cavity, the *atrium*, which opens externally by the *atriopore*. In respiration and feeding, the sea water containing unicellular and other minute organisms is drawn through the mouth from the cavity formed by the hood and its extended *cirri*. From the pharynx the excess water passes through the gill slits into the atrium and out by the *atriopore*, the microorganisms being retained as food and passing to the intestine, as they do in tunicates. The action of cilia upon the gill slits and elsewhere is principally responsible for this flow of water that sifts out the food material and functions in respiration. The *circulatory system* consists of a ventral blood vessel, which extends the length of the digestive tract, and a dorsal vessel, which is divided into right and left branches in the region of the pharynx. The dorsal and ventral vessels are connected anteriorly by vessels in the walls of the pharynx and posteriorly by a network of vessels in the digestive tract and body wall. There is no heart, and circulation is effected by peristaltic contractions of the larger vessels. The course of the blood ante-

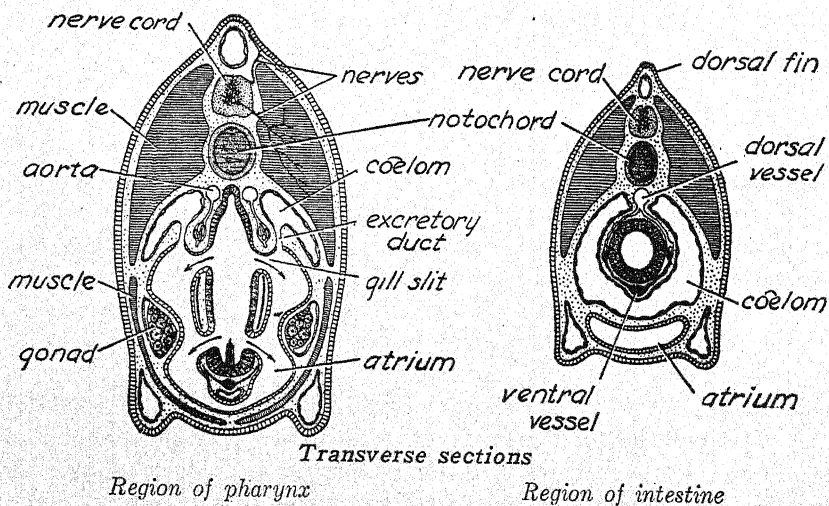
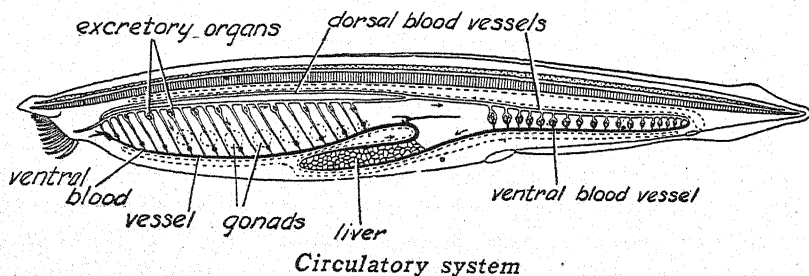
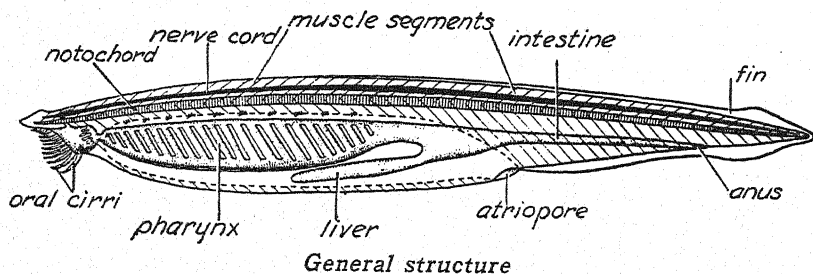


FIG. 436. Structure of amphioxus.

(Modified from Stempel, "Zoölogie im Grundriss," 1926.)

riorly in the ventral vessel, posteriorly in the dorsal vessel, and through the dorso-ventral connections resembles the course in vertebrate embryos and in fishes (*cf.* Fig. 19, p. 39). There is a conspicuous *cœlom* in the region of the intestine, but anteriorly the *cœlom* is reduced in relation to the space occupied by the pharynx. Numerous *excretory organs*, in the form of modified nephridia, open into the atrium; they occur in pairs and are arranged metamerically. A relatively large part of the body, as seen in the intestinal region, is occupied by the general musculature. In the pharyngeal region this musculature, like the *cœlom*, is restricted principally to the dorso-lateral portions of the animal. Surrounded by this musculature and dorsal to the digestive tract is the *notochord*, in a position comparable to that of the notochord of vertebrate embryos (*cf.* Fig. 86, p. 146). The connective tissue sheath surrounding the notochord is extended dorsally as a sheath for the *central nervous system*, which is tubular, like the nervous system of a vertebrate. The cavity of this tube is slightly expanded at the anterior end, where there is a supposedly olfactory organ and a median pigment spot. There is no anterior differentiation of the cord that can be fairly called a brain, although two pairs of nerves that extend anteriorly have been termed cranial nerves. Posterior to them a large number of nerves pass from the nerve cord in a metameric arrangement corresponding with that of the muscle segments. The cord contains *photo-receptors* in the form of pigmented, cuplike bodies. The *reproductive organs* consist of paired gonads, arranged metamerically and projecting into the atrium. The sexes are separate, and the gametes are discharged into the atrium by rupture of the gonad walls. From the atrium they pass through the atriopore to the external water, where fertilization occurs. The development of the amphioxus has been described in Chapter 5 (*cf.* p. 138).

The chordate features of the Amphioxi are apparent from the foregoing description. The dorsal, tubular nervous system arises from the dorsal ectoderm (Fig. 81, p. 138). The notochord is obviously comparable to the structure of this name which occurs in vertebrates. The gill slits, the arrangement of blood vessels, and the course of the blood flow, along with other resemblances, mark these animals as chordates, although much simpler in their organization than the primitive fishes.

The Acraniata thus include one group, Hemichordata, in which the supposedly chordate features are such that some taxonomists place these animals by themselves in a minor phylum, and two groups, the Urochordata and Cephalochordata, which are more closely related to each other, although they are widely divergent types. An attempt to

relate Acraniata with Craniata through a common ancestry takes us far back of the Cambrian (*cf.* Fig. 469, p. 646), and, since we have no fossils to help us piece out the story, there is no evidence except that from comparative anatomy and embryology.

The Craniata or Vertebrata

A *skull*, or cranium, and *vertebræ* are the features that have given the names Craniata and Vertebrata, respectively, to these animals. Enclosed by the skull is a *brain*, which is formed by differentiation of

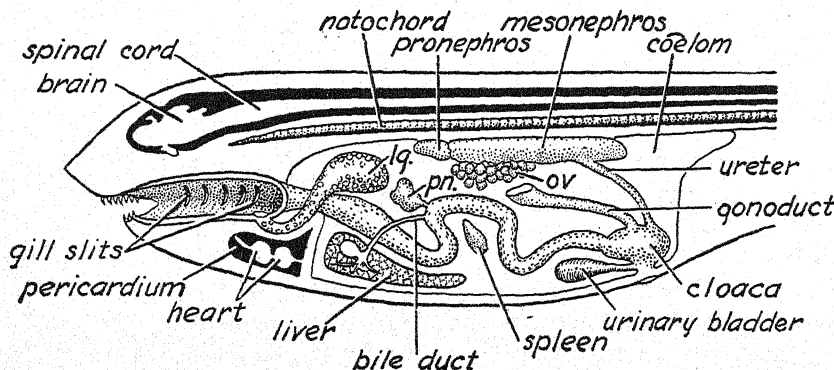


FIG. 437. Diagrammatic longitudinal section of a vertebrate, with female reproductive organs: *lg.*, lung; *ov.*, ovary; *pn.*, pancreas.

(Redrawn from Wiedersheim, "Comparative anatomy of vertebrates," copyright, 1907, by the Macmillan Co., reprinted by permission.)

the anterior end of the neural tube (*cf.* Fig. 86, p. 146). In correlation with the development of the brain and its encasing skull the notochord does not extend to the very anterior end of the body, as in the amphioxus. The *notochord* always appears in development, and in many of the lower vertebrates it persists in the adult as a cord running through the center of each vertebra. In higher forms the *vertebræ* completely replace this primitive axial skeleton. The great majority of species have paired *appendages*, fins, or limbs. The pharynx is of moderate size, and the *gill slits* are transitory in the lung-breathing vertebrates. There are a well-developed *heart* and blood with *red cells*. Paired *eyes* and *ears*, cranial and spinal *nerves*, a *cœlom*, and a single pair of *gonads* are additional features characteristic of the Vertebrata. The representation of a generalized vertebrate, in Figure 437, illustrates some of these relationships. Separation of the Vertebrata into gill-bearing forms with fins, the *Pisces*, and air-breathing forms with

limbs, the *Tetrapoda*, is in accordance with the evolution of these animals from an aquatic to a terrestrial mode of life (cf. Fig. 445).

The Pisces or Fishes. As the first type of vertebrates that is known from the fossil record, the Pisces have had a long and diversi-

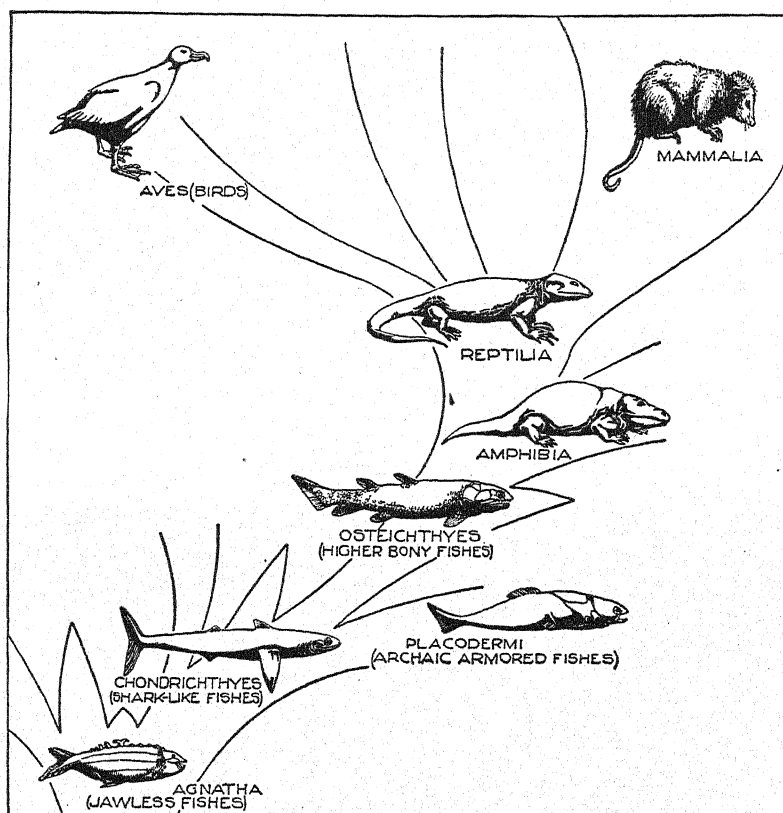


FIG. 438. Simplified family tree of the vertebrates.

(From A. S. Romer, "Man and the vertebrates," copyright, 1933, by University of Chicago Press, reprinted by permission.)

fied history. There are reasons for believing that the earliest known fishes, which are called Ostracodermi (Fig. 439), lived, and perhaps originated, in fresh water and that the ocean was subsequently invaded by some of their descendants, which thus became the first marine fishes. The earliest complete skeletons of Ostracodermi have been found in the Silurian, although numerous bony scales from the Ordovician are regarded as fragments from such animals. In the Devonian the modern types had appeared as primitive sharks repre-

senting the Chondrichthyes, along with primitive representatives of the Osteichthyes.

The Agnatha, or Jawless Fishes. The lampreys and hagfishes (Fig. 439), which are the only living members of the Class Agnatha, are round-mouthed and jawless, with a single nostril on the dorsal side

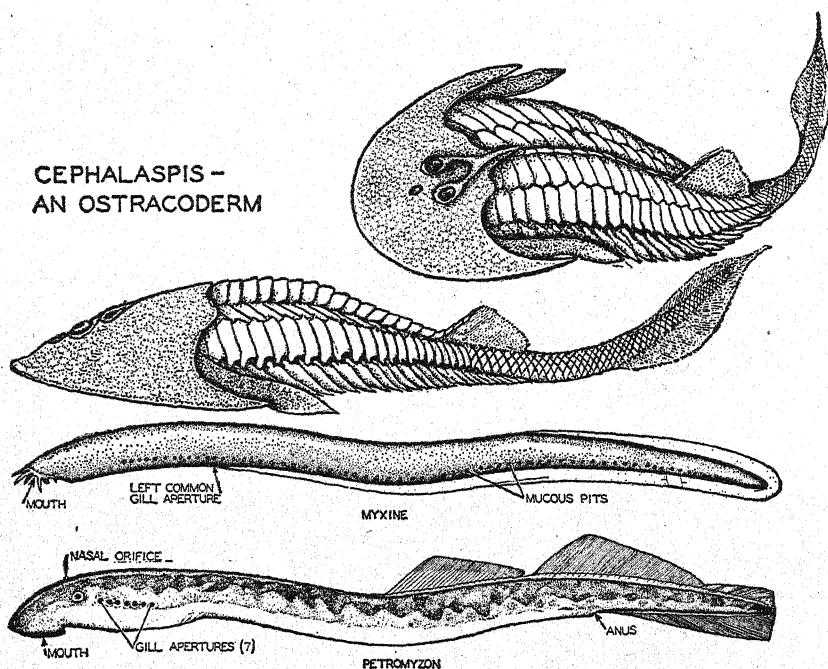


FIG. 439. Representative Agnatha (Cyclostomata) or jawless fishes. *Above*, the extinct ostracoderm, *Cephalaspis*. *Middle*, the hagfish, *Myxine*. *Below*, the lamprey, *Petromyzon*.

(From Neal and Rand, "Comparative anatomy," copyright, 1936, by P. Blakiston's Son and Co., reprinted by permission.)

of the head, *without appendages*, with a persistent *notochord*, and with *rudimentary vertebræ*. Also classed as Agnatha are the extinct Ostracodermi, which were round-mouthed and jawless and in some of which the single nostril was apparent. It appears that the hags and lampreys of the present time are lone survivors from the earliest type of fishes, although they represent a highly specialized and perhaps a degenerate type. A lamprey feeds by attaching its suckerlike mouth to the surface of another fish and tearing off the flesh with its inner mouthparts. The mouth is also used for holding to stones in swift water. The hags likewise feed upon other fishes, becoming attached and boring their way

into the flesh to such an extent that they can almost be regarded as internal parasites. Both these types are represented by only a few genera distributed in the ocean and in fresh water.

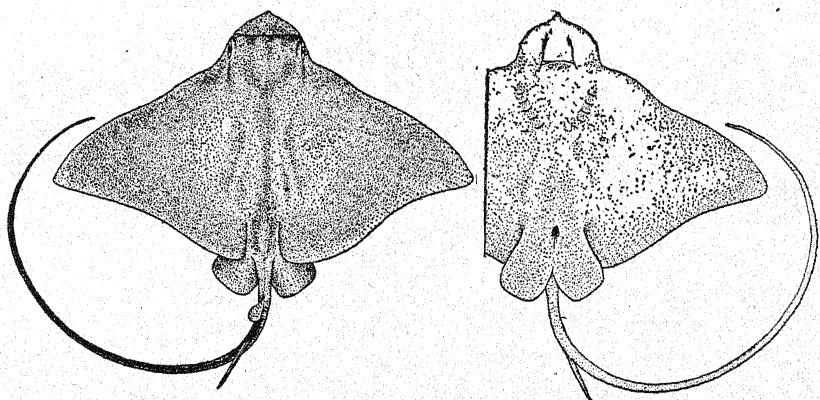
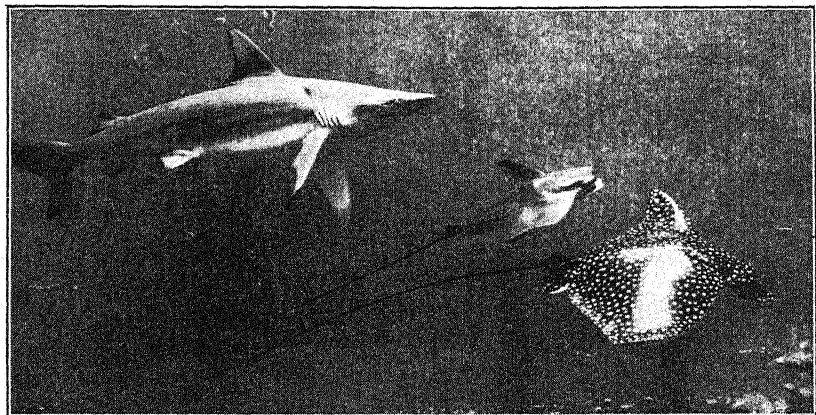


FIG. 440. Representative Chondrichthyes (Elasmobranchii) or cartilaginous fishes. The gill slits, which are exposed and not covered with an operculum as in bony fishes, should be noted. *Above*, shark and rays. *Below*, sting-ray from dorsal and ventral views.

(*Above*, from group in Field Museum of Natural History, Chicago; courtesy of the Museum. *Below*, from New Jersey State Museum, Annual Report, 1906.)

The Chondrichthyes. This class includes the dogfish, sharks, skates, and rays (Fig. 440). These fishes, in contrast to the Osteichthyes, have a cartilaginous skeleton, long regarded as the survival of a very primitive feature in the evolution of vertebrates. It now appears that the earliest known Chondrichthyes had bony skeletons. Hence, the exist-

ing forms seem to represent a line of descent in which the skeleton has degenerated from an earlier bony type to its present cartilaginous state. Biting *jaws*, *teeth*, and paired *fins* are obvious specializations beyond those of the Agnatha. The jaws are regarded as having arisen from skeletal bars of the gill region, and the teeth from scales similar to those in the skin of a modern shark. The origin of the paired fins is problematical. Sharks' teeth and remnants of the exoskeletons, which were well developed in many of the early forms, are much more abundant as fossils than are other remains of these animals, presumably because other parts of their skeletons had little chance for preservation. However, the fossils in some of the Devonian deposits enable the paleontologist to make fairly complete reconstructions of types that were primitive yet specialized in their own ways. The primitive sharks apparently originated in fresh water, from some line of the ostracoderms, and subsequently migrated to the ocean, disappearing from fresh water. Ever since this invasion sharks of many sorts have been among the largest of the marine fishes and are now familiar predators of surface waters in the ocean, where they attack a wide range of prey (Fig. 149, p. 230). The dogfish is merely a small type of shark. The skates and rays, with their specialization for bottom life in the ocean, represent a more divergent type. They live commonly in shallow waters, feeding upon mollusks, crustaceans, and other sluggish animals of the bottom. The sting-rays (Fig. 440 Below) have spines upon the tail and related poison glands. The venom introduced into lacerations produced by these spines is poisonous and sometimes fatal to representatives of all the classes of vertebrates including man. The torpedo-ray has a large organ on each side of the body that discharges electricity whenever the living fish is touched.

The Osteichthyes. In contrast to the existing Agnatha and Chondrichthyes, with their cartilaginous skeletons, members of the Class Osteichthyes (Figs. 441-444), have bony skeletons, although the bones of this skeleton are not as firmly articulated as the bones of land vertebrates. Bone did not appear first with the Osteichthyes, since it was present in the skeletons of early Agnatha (Figs. 438 and 439) and Chondrichthyes. The first representatives of the Osteichthyes appear in the middle Devonian, soon after the earliest sharks. These early Osteichthyes are separable into two groups, the *ray-finned* and the *lobe-finned fishes*. From these ray-fins descended the ray-finned fishes of the present day (Figs. 441 and 442). From the lobe-fins there have descended the land vertebrates (Tetrapoda) and the existing lungfishes, called Dipnoi (Fig. 443).

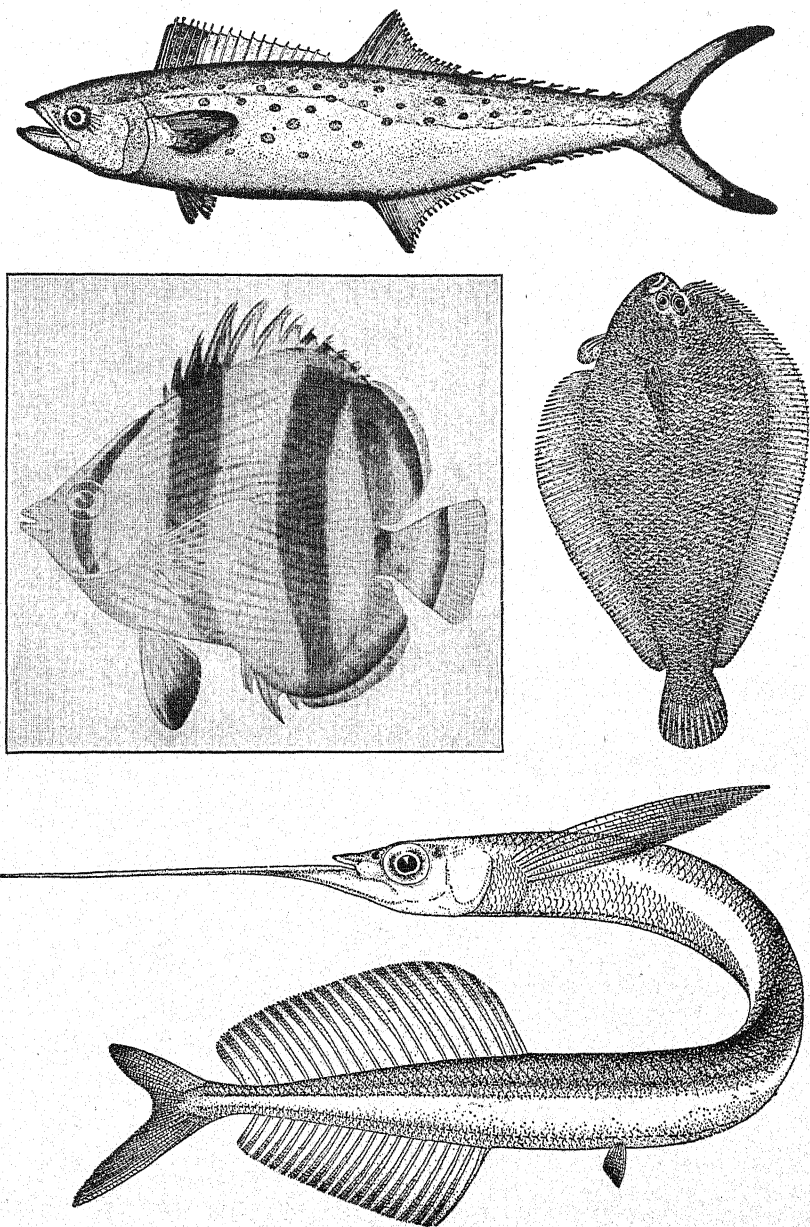


FIG. 441. Osteichthyes (Teleostomi). Above, Spanish mackerel, *Scomberomorus*. Middle-left, butterfly-fish, *Chaetodon striatus*. Middle-right, little flounder, *Etropus microstomus*. Below, ribbon half-beak, *Euleptorhamphus velox*.

(Above, from Neal and Rand, "Comparative anatomy," copyright, 1936, by P. Blakiston's Son and Co., reprinted by permission. Others, from New Jersey State Museum, Annual Report, 1906.)

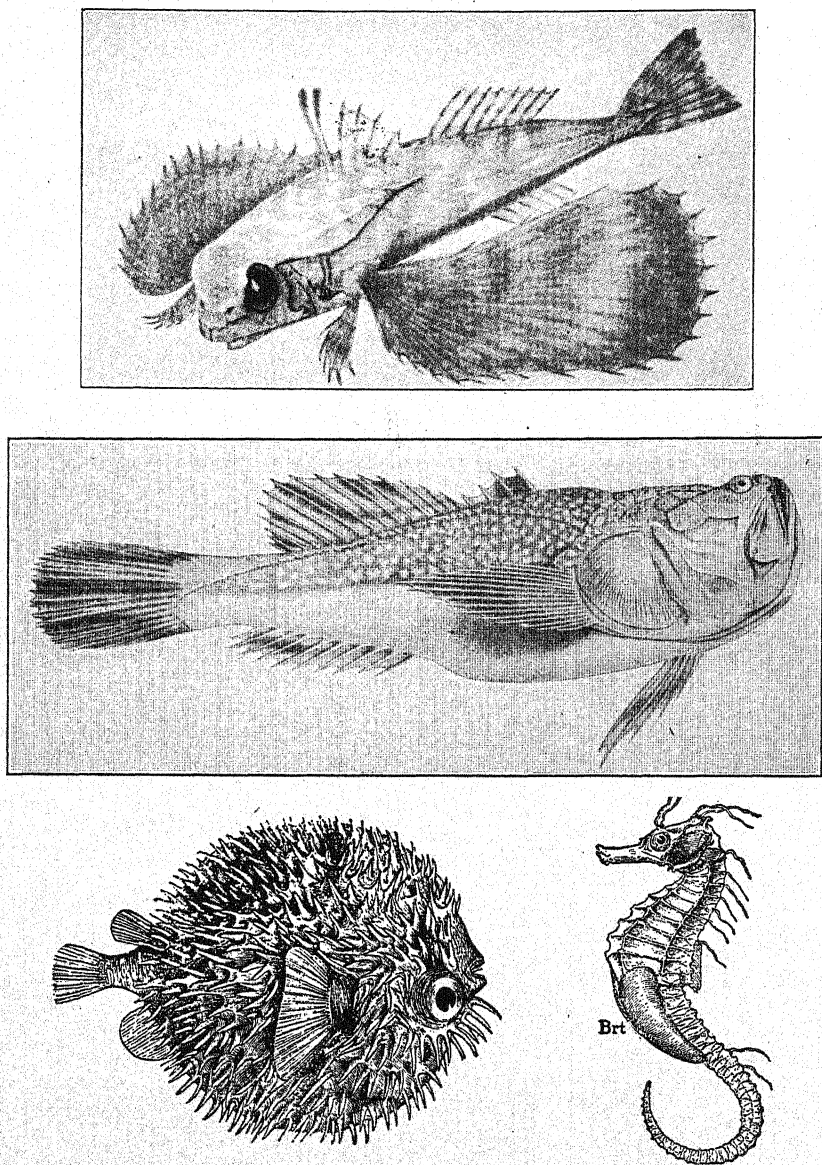


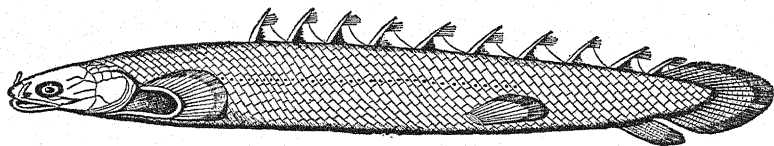
FIG. 442. Osteichthyes (Teleostomi). Above, flying gurnard, *Cephalacanthus volitans*. Middle, northern stargazer, *Astroscopus guttatus*. Below-left, hedgehog fish, *Diodon maculatus*, distended with air and floating ventral side uppermost. Below-right, male seahorse, *Hippocampus antiquorum*, showing brood-pouch (Brt).

(Above, from William Beebe, 1928, *Natural History*, vol. 28. Courtesy of American Museum of Natural History. Middle, from New Jersey State Museum, *Annual Report*, 1906. Below, from W. Stempell, "Zoölogie im Grundriss," 1926.)

Surprising as it may seem, a *lung* or *lungs* appear to have been present in many, if not all, of these early fishes, perhaps as an adaptation to life in stagnant pools that may have been formed recurrently in the watercourses under the climatic conditions of the Devonian. Apparently the *swim bladder* of modern bony fishes, which is homologous with the lungs of tetrapod vertebrates, is not the organ from which lungs arose but a modification of the primitive lung in the early ancestors of these fishes. After making a beginning of air-breathing, it appears that one line, the lobe-finned fishes, gave rise to the Amphibia and so the land vertebrates before it became extinct, whereas another line, the ray-finned fishes, gave rise to the bony fishes of the present day, in which the primitive lung was transformed into a hydrostatic organ, the swim bladder.

It is significant in this connection that in the most primitive of existing ray-finned fishes, such as the "bichir" of the Nile, *Polypterus* (Fig. 443), the lung still persists in its original function. Another and independent survival of the primitive lung appears in the three genera of lungfishes (*Dipnoi*), *Ceratodus*, *Protopterus*, and *Lepidosiren* (Fig. 443). In North America the sturgeon, *Acipenser*, the paddle fish, *Polyodon*, the gar pike, *Lepidosteus*, and the bow-fin, *Amia*, are ray-fins of primitive type, although they do not have lungs as does the more primitive *Polypterus*. The more specialized ray-fins include all the most familiar fishes of fresh and salt water, such as the trout, salmon, carp, bass, perch, catfish, cod, herring, mackerel, and many others that are highly specialized. Although they are all modifications of the ray-finned type of fishes, the diversity of these forms is bewildering, as may be appreciated by visiting a public aquarium or by turning the plates of some monograph. Almost every kind of shortening, lengthening, and flattening can be found in one species or another, along with such modifications as those of the pipe-fish, toad-fish, sea-horse, flying fish, flounder, and the luminescent fishes of the depths (Figs. 441 and 442).

The lungfishes known as *Dipnoi* are not closely related to the lungfishes represented by the primitive ray-fin, *Polypterus*, in which lungs have likewise survived from the lungs of the early bony fishes (Fig. 443). The *Dipnoi* represent another and independent survival of lungs from the early ancestors. They are a remnant of a numerous race of similar forms that lived during the Age of Fishes. Of the three surviving genera, *Ceratodus* occurs in Australia, *Protopterus* in South Africa (Fig. 443), and *Lepidosiren* in South America. *Ceratodus* lives in quiet reaches of its native streams, where the water becomes stagnant and the plant growth is heavy in the dry season.



POLYPTERUS

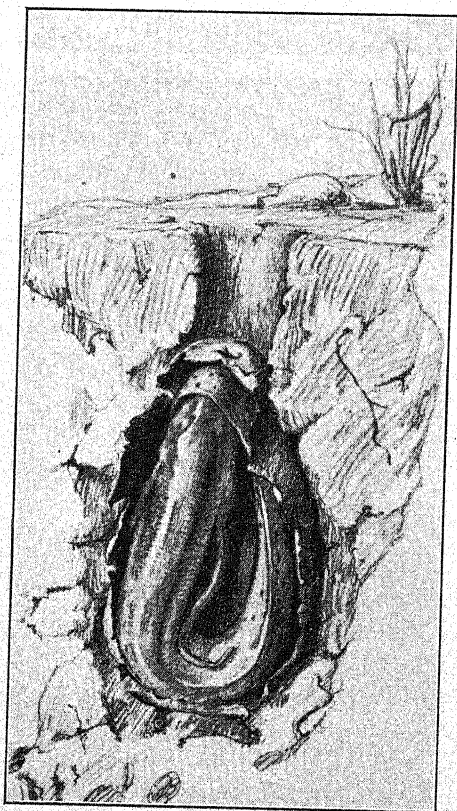
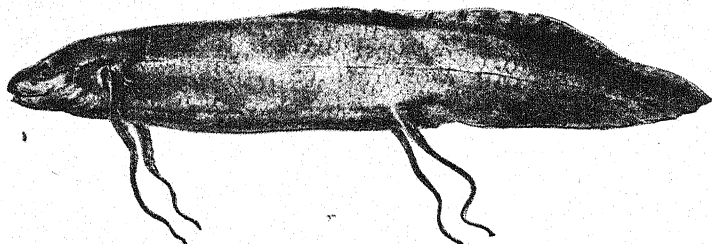


FIG. 443. Existing lungfishes. *Above*, the "bichir" of the Nile, *Polypterus*, a ray-finned teleost with a primitive organization. *Middle*, the South African lungfish, *Protopterus annectens*, one of the Dipnoi which are also teleosts. *Below*, *Protopterus*, at the bottom of its burrow, surrounded by an encasement of dried slime, in which the fish remains during the long, dry season, becoming active again with the next rainy season.

(*Above*, from Neal and Rand, "Comparative anatomy," copyright, 1936, by P. Blakiston's Son and Co., reprinted by permission. *Middle*, after Dean in Parker and Haswell, "Textbook of zoölogy," copyright, 1921, by Macmillan and Co., Ltd., reprinted by permission. *Below*, from F. LaMonte, 1932. Natural History, vol. 32; courtesy of American Museum of Natural History.)

Under these conditions its gills furnish insufficient respiration, and it must come to the surface periodically and take air into its lung. It cannot survive if the pool becomes entirely dry. Its food consists of the aquatic vegetation, both living and decomposing. It is typically sluggish in its reactions and in this respect more like a salamander than one of the active fishes. The respiration by the gills, which are like those of other fishes, must be supplemented by that of the lung, which is a bilobed and single organ in *Ceratodus* instead of being a paired organ as in the other lungfishes. In contrast with *Ceratodus*, *Protopterus* and *Lepidosiren* burrow into the mud when the stream dries completely and can survive a long drought. Even in its active state, *Protopterus* will drown if kept under water. It is clear from the fossil record that the Dipnoi descended from some of the oldest lobe-finned fishes, but not from the type of lobe-fins that gave rise to the land vertebrates. They represent an independent line of evolution from gill-bearing toward lung-bearing forms and so terrestrial habits.

The Pisces living and extinct are thus the basic type among vertebrate animals, appearing first in the fossil record and including at the present time descendants of Devonian types, such as the sharks, that are flourishing if not large groups, and also groups living and extinct that suggest the beginnings of vertebrate life on the land. Originating in fresh water, so far as the fossil records indicate, the Pisces seem to have invaded the ocean and since that time to have inhabited both fresh and salt water. The story of the ancient lung-breathers, from which land vertebrates arose and whose lung-breathing has survived in the two independent lines of lung-breathing fishes, is paralleled by other fishes "coming out of the water" in a great variety of ways in response to the struggle for existence along recent shore lines (Fig. 444). At the other extreme are the fishes that have invaded the depths of the ocean and been modified no less remarkably than those which invaded the land and whose descendants became the land-dwelling vertebrates.

The Tetrapoda or Four-footed Vertebrates. Until recently the earliest trace of a land vertebrate was the supposed imprint of a foot in the upper Devonian of Pennsylvania; but within recent years skeletal remains of very primitive amphibians have been found in the late Devonian of Greenland, confirming the belief that the well-developed forms of the Carboniferous deposits (Fig. 446) were preceded by earlier amphibians in the Devonian or Silurian. The evolution of these earlier amphibians must have involved a long period of transition during which *fins* became *limbs* and *air-breathing* became increasingly

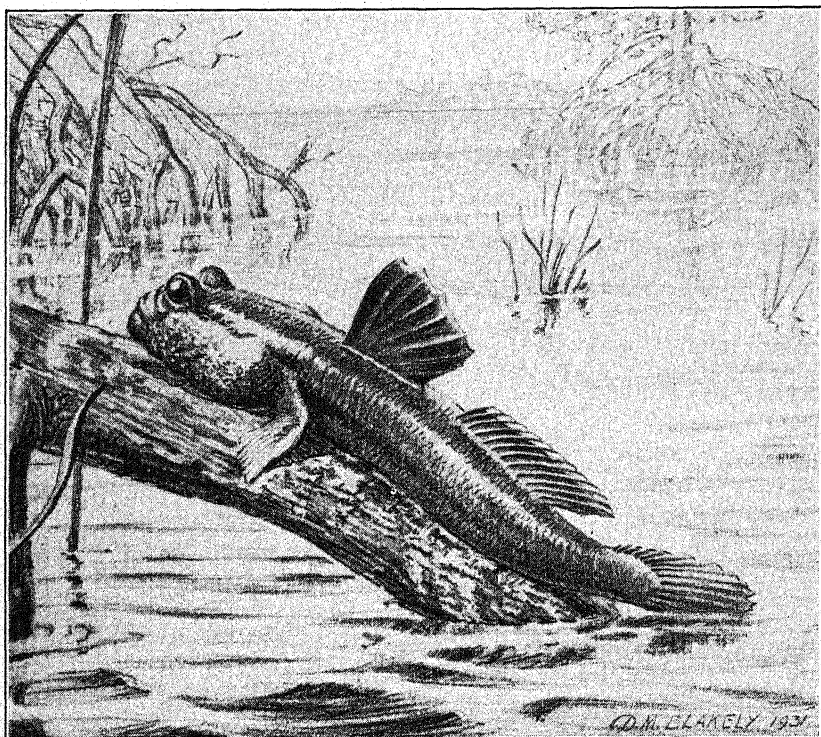
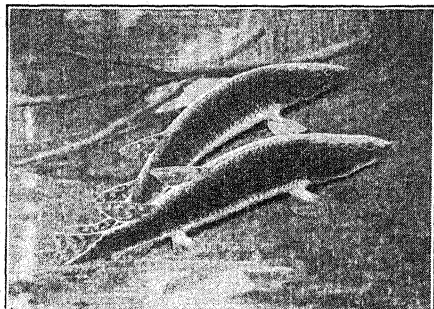


FIG. 444. Fishes coming out of the water. *Above*, reconstruction of the primitive lobe-finned fish, *Eusthenopteron*, which is supposedly like the lobe-fins that took to the land and became the ancestors of amphibians. *Below*, mudskipper, *Periophthalmus*, in a mangrove swamp, an existing fish that often takes to the land when pursued in shallow water, using its pectoral fins effectively in terrestrial locomotion and having eyes adapted for vision in air as well as water.

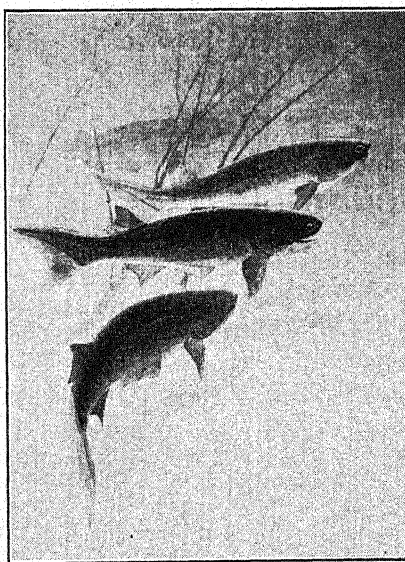
(*Above*, from W. K. Gregory, 1937, *Natural History*, vol. 39. *Below*, from F. LaMonte, 1932, *Natural History*, vol. 32. Both by courtesy of American Museum of Natural History.)



Primitive reptile, *Seymouria*.



Mammal-like reptile, *Cynognathus*.



Primitive ganoid fish, *Cheirolepis*.



Generalized amphibian, *Diplovertebron*.

FIG. 445. Reconstructions of representative types in the evolution of vertebrates from primitive fishes to primitive mammals.

(Courtesy of American Museum of Natural History.)

important in respiration. It is clear that the first land vertebrates were Amphibia and that they arose from lobe-finned fishes (cf. Figs. 444 and 445). It will be recalled that these lobe-fins were already provided with lungs; the bones of their fins may also be compared with the bones of the limbs in amphibians (Fig. 447). From these primitive four-footed land animals have descended all the terrestrial vertebrates of later times. If we put together what we know from the fossils and from the geological formations, it seems probable that the factors influential in the change of habitat from water to land and in the evo-

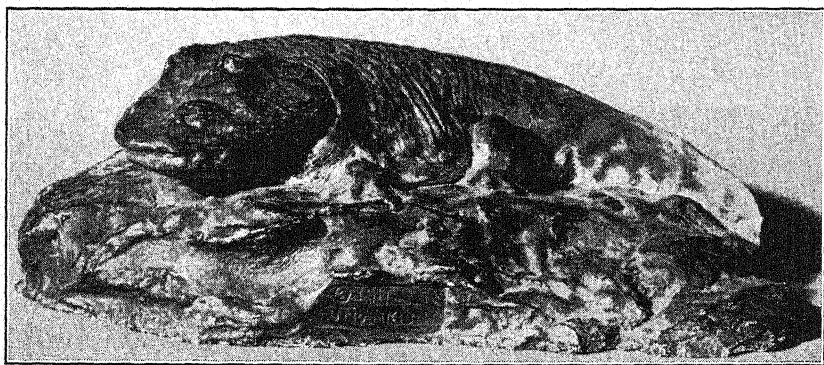


FIG. 446. Reconstruction of the stegocephalian, *Eryops*.

(From model by D. Frankline; courtesy of American Museum of Natural History.)

lution from four-finned to four-footed vertebrates were such that early land animals were led to seek water rather than land. Droughts appear to have been frequent in the Devonian; it is thought that forms capable of moving across country "when the food failed and the last water dried" survived, whereas those that persisted as lobe-fins gradually became extinct. Whatever may have been the course of events, the changes in structure and habitat were effected. With the spread of these early land forms and the decline of the fishes came the Age of Amphibians as the first act of the evolutionary drama during which the four-footed vertebrates came to possess the land (Figs. 445 and 452).

The Amphibia. Even today the amphibians remain half water- and half land-dwellers; they lead a "double life," as their name indicates (Fig. 450). Although they are typically vertebrates with well-developed *lungs*, this mode of respiration is supplemented by *cutaneous respiration* in most species. Moreover, the *tadpole* stage of amphibians is fishlike not only in structure but also in habitat and activities. There are, of course, other features characteristic of the

Class Amphibia, but they need not be considered for our present purpose. The earliest amphibians available as fairly complete skeletons resemble the lobe-finned fishes, on the one hand, and the reptiles, on the other. It appears that such amphibians gave rise to certain specialized types that became extinct, to the ancestors of modern amphibians, and to the ancestors of reptiles. Among the primitive types were those called Stegocephalia, or "roof-headed," because of their armored skulls (Fig. 446); other forms were lean and active swimmers, if one may judge from their skeletons. The conspicuous dermal plates, like those

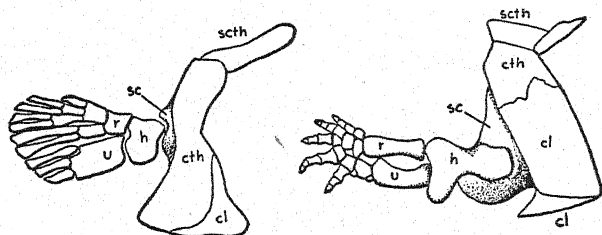


FIG. 447. The right pectoral limb, or arm, and shoulder region of a lobe-finned fish (*left*) and of a primitive amphibian (*right*), the latter turned back to a position comparable with the fish's fin. As indicated by the lettering, the bony units of the two are comparable (*cf.* Fig. 36, p. 67).

(From A. S. Romer, "Man and the vertebrates," copyright, 1933, by University of Chicago Press, reprinted by permission.)

of fishes and reptiles, which were present in many of these early forms have been lost in existing amphibians. Although the limbs were used in locomotion, they did not carry the weight of the body, which still trailed along the ground, presumably aiding the locomotion by its sinuous movement, as in the modern salamanders. In like manner the separation of oxygenated from unoxygenated blood was, presumably, incomplete, as it is in the amphibians of today (*cf.* p. 39). With the divergence of the reptilian line, the extinction of the aberrant types, and differentiation of the surviving lines, the evolution of the modern forms was well on its way when the Age of Amphibians drew to a close. With no other large land animals as competitors and with the swampy conditions that prevailed in carboniferous times, the Amphibia flourished. Competition with the reptiles, as a type better adapted for terrestrial life, and the advent of a drier land surface were perhaps important factors in the amphibian decline toward the close of the Permian. In any event the Amphibia of today are small in size and few in number by comparison with those of the past. They have survived, like a whole group of "living fossils," in so far as they represent the

fishes that once walked upon the land, but presumably returned to the water for their development.

Among existing Amphibia the most generalized are the *Caudata*, or tailed forms, such as the salamanders, *Amblystoma tigrinum* (Fig. 147, p. 228) and *Necturus maculosus*, and the newt *Triturus* (*Diemyctylus*) *viridescens*. *Amblystoma* apparently lives most of the year upon the land, going to the water for breeding in the spring. *Triturus* lives in

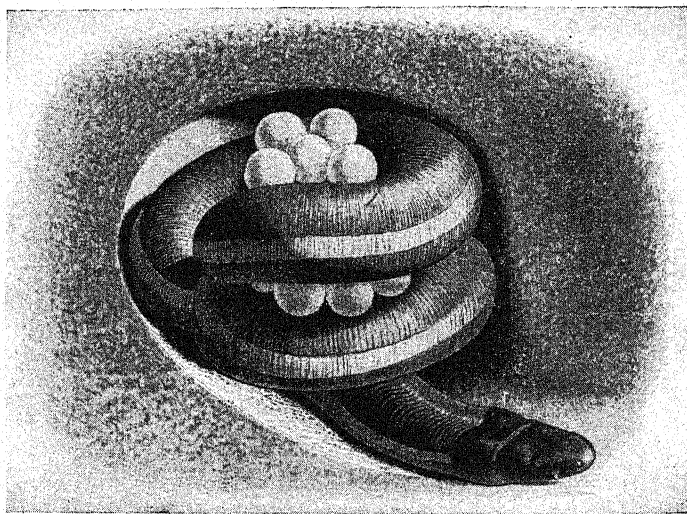


FIG. 448. The limbless amphibian, *Ichthyophis*, and its eggs, as it appears in its burrow; about natural size. The eggs, in their gelatinous capsules, develop in the moist atmosphere of the burrow instead of in water as do the eggs of most amphibians.

(After Sarasin in A. S. Romer, "Man and the vertebrates," copyright, 1933, by University of Chicago Press, reprinted by permission.)

the water as an adult and breeds there, but the early juvenile stages are passed on land. *Necturus* can live only in the water, since its respiration depends upon gills which are comparable with the external gills that occur temporarily in the development of other amphibians. An extreme type among the Caudata is the "Congo snake," *Amphiuma means*, of the southeast quarter of the United States, which may reach a length of 3 feet and in which the limbs are so reduced that the heavy-bodied animal is snakelike in appearance; another is the "hell-bender," *Cryptobranchus alleganiensis*, of the eastern United States; and another the giant salamander, *Megalobatrachus maximus*, of Japan, which is the largest of existing amphibians, although it attains a length of less than 6 feet.

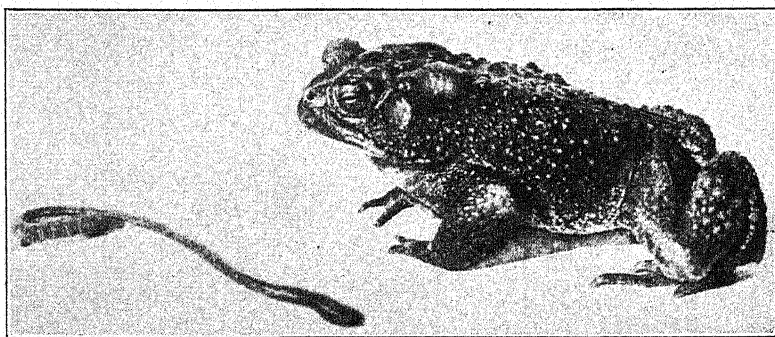


FIG. 449. The American toad, *Bufo americanus*. Above, a male with buccal sacs expanded in "singing." Middle, capturing an insect with the tongue. Below, "stalking" an earthworm.

(From M. C. Dickerson, "Frog book," copyright, 1920, by Doubleday, Page and Co., reprinted by permission.)

The order *Apoda*, or limbless amphibians, is represented by a few small forms found only in the warmer parts of the world (Fig. 448). They burrow in the ground and are about the size of large earthworms. Their limbless state is a highly specialized characteristic, but in more important internal features they are the most primitive of living amphibians.

The most familiar amphibians are included in the Order *Salientia*, or "leapers," which comprises the many species of frogs and toads (Figs. 449-451). The line of descent for this modern type was indicated at the close of the Age of Amphibians, but they were not clearly differentiated in their present form until the Age of Reptiles was well advanced. Existing species of *Salientia* are distributed to all the continents, in the tropics as well as temperate latitudes and as far north as the ground does not remain frozen throughout the year. On the whole they are the most specialized of the modern forms, as their greatly developed hind limbs and the absence of a tail in the adult bear external witness. Most species can live for long periods out of the water if the atmosphere is sufficiently moist. Some are more nearly land animals than any other amphibians. For example, the toad, *Bufo americanus* (Fig. 449), lives on land except when it goes to the ponds during its brief breeding season in the spring, but it can survive only in a moist atmosphere. For this reason toads are seldom seen during a drought. At such a time they remain in shaded places or in the holes to which they retire in the daytime. The frogs are even more dependent upon water and a moist atmosphere because of their greater need for cutaneous respiration.

Among the species of frogs common in the eastern and central portions of the United States the bullfrog, *Rana catesbiana*, and the green frog, *R. clamitans*, have similar habits and are confined to the vicinity of water (Fig. 450). The leopard frog, *R. pipiens*, on the other hand, may wander far from water and is sometimes called the grass frog because it is found in meadows. The pickerel frog, *R. palustris*, may also wander from the water, although it lives mostly in spring beds and in cool, damp places. A more extreme example is the wood frog, *R. sylvatica*, which is regularly found in damp woods, often a long distance from water. Like the toad, it comes to the water at the breeding season, and in wet weather it has access to temporary ponds. *Acris gryllus*, the cricket frog, is another pond- and stream-dwelling species, occurring usually in swampy places and in small bodies of water. *Hyla versicolor*, the tree frog (Fig. 451), comes to the water in numbers only at the breeding season and frequents damp places at other times, climbing tree trunks to feed upon insects. It changes

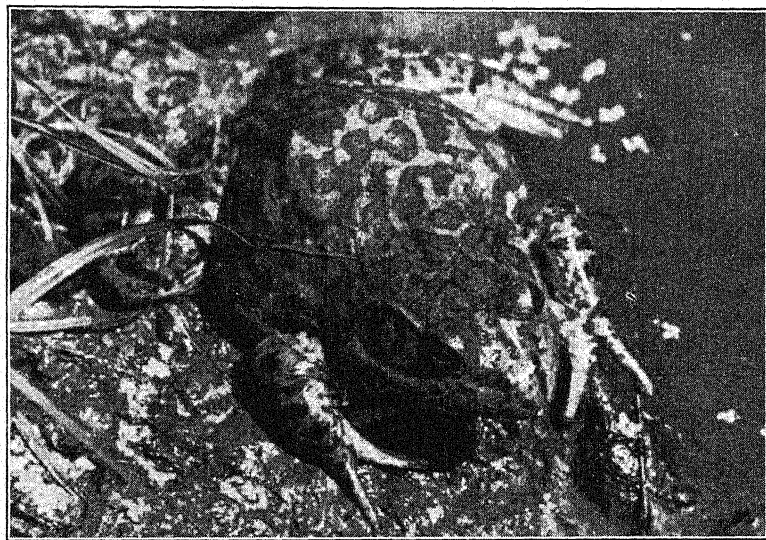
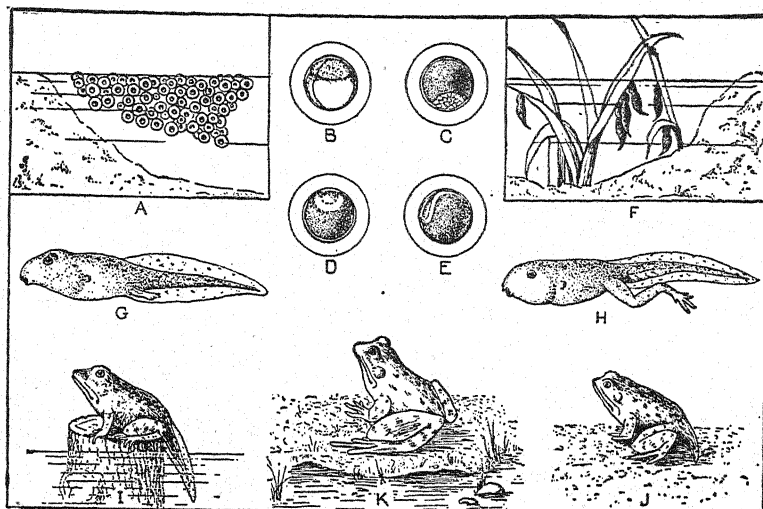


FIG. 450. The frog and its life-cycle. *Above*, stages of life-cycle. *A*, eggs. *B*, *C*, *D*, and *E*, cleavage, gastrula, and neuralfold stages. *F*, newly hatched tadpoles. *G* and *H*, later tadpole stages. *I*, *J*, and *K*, metamorphosis to juvenile frog. *Below*, a frog in its normal land-and-water environment.

(*Below*, from a photograph by Charles Schwartz.)

color to match the background, which probably accounts for the fact that these animals are difficult to locate, although their croaking is often heard, particularly when the atmosphere is saturated with moisture before a rain.

The general distribution of the amphibians is, therefore, conditioned by the needs of each species in connection with cutaneous respiration and the correlated adaptation of the skin for this function, and by their aquatic breeding habits. None of these forms is truly a land animal like the reptile, which lives and breeds in a hot, dry place.

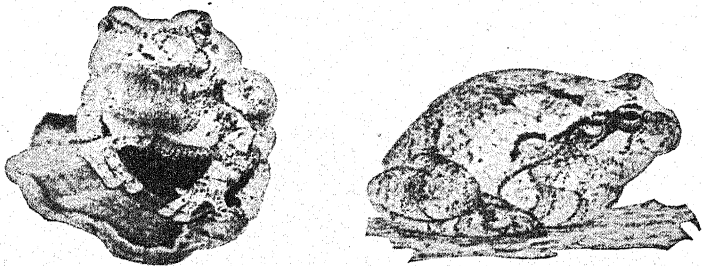
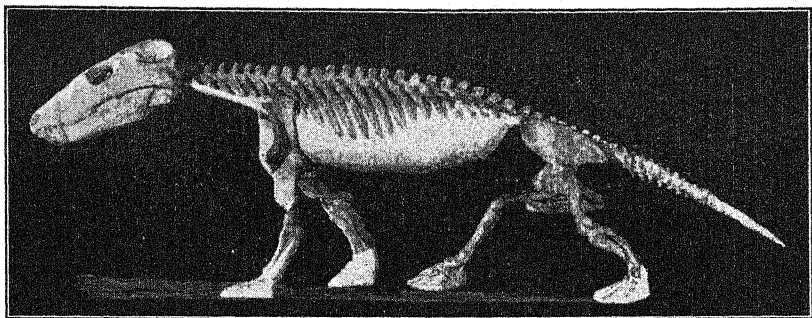


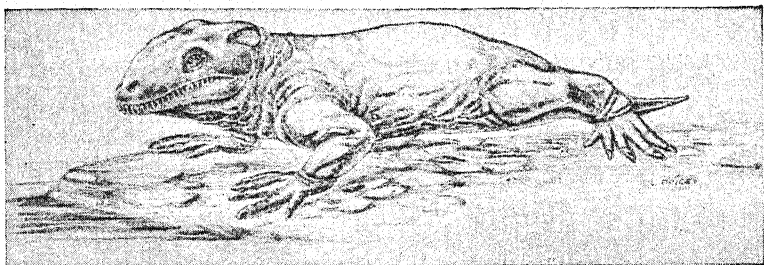
FIG. 451. The common tree frog, *Hyla versicolor*, showing mottled coloration that matches its background in nature.

(From M. C. Dickerson, "Frog book," copyright, 1920, by Doubleday, Page and Co., reprinted by permission.)

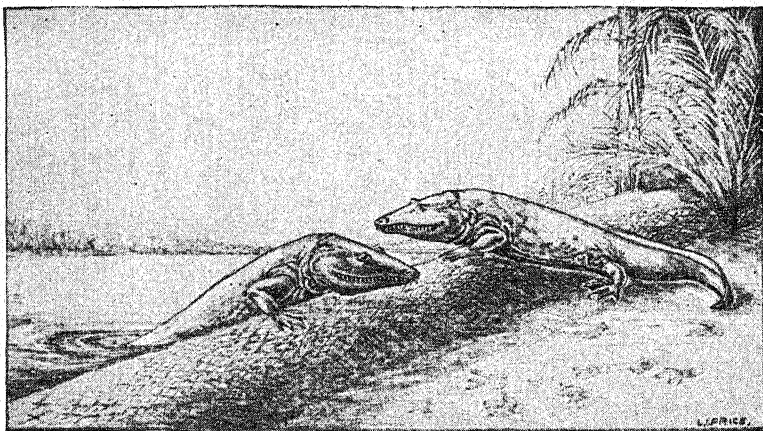
The Reptilia. Reptiles are *cold-blooded*, *air-breathing* vertebrates characterized by the development of horny *epidermal scales* and often with an underlying armor of bony *dermal plates*, along with other, less obvious features of internal anatomy. In contrast with amphibians, which are typically dependent upon a moist atmosphere and upon water for their egg-laying, the reptiles are thoroughgoing land animals. Not only can they live upon the land, even under desert conditions, but they also develop upon it. Air-breathing, a skin and an egg-membrane resistant to drying, and certain modifications of the embryonic development are the features that make possible this complete adaptation for terrestrial life. Arising from Amphibia, they became the dominant land animals in the Age of Reptiles and gave rise to the birds and to the mammals (Fig. 452). Their manner of development, as compared with those of amphibians and of mammals, represents an important step in vertebrate evolution (Fig. 445). Most reptiles are *oviparous* (Fig. 454 and p. 620). The reptilian embryo develops in a fluid medium, as does the amphibian, but the medium for the reptile is the watery fluid enclosed within a sac of embryonic tissue and surrounded by the protective egg-membrane.



Cynognathus, a mammal-like reptile; regarded as the earliest of known mammalian types.



Seymouria, the most primitive of known reptiles; from the lower Permian.



Diplovertebron, a primitive paleozoic amphibian.

FIG. 452. Extinct types representative of the evolution of land-dwelling vertebrates.

(Above, from W. K. Gregory, 1937, *Natural History*, vol. 39. Courtesy of American Museum of Natural History. Middle and Below, restorations by Llewellyn Price, from A. S. Romer, "Man and the vertebrates," copyright, 1933, by University of Chicago Press, reprinted by permission.)

In correlation with a much larger amount of yolk than is found in the eggs of amphibians, the hatching period in reptiles is delayed until the young have reached the stage of juveniles able to care for themselves as do newly hatched turtles and alligators (Fig. 454). Some reptiles have been modified from this state and have become *ovoviviparous*. When mammalian development is compared with that of reptiles, it is evident that the viviparous development of most mammals has been evolved from an oviparous state like that of reptiles. Indeed, the lowest mammals, such as the duckbill and the spiny anteater (Fig. 462), still lay eggs.

The earliest known reptiles are from the Carboniferous. These primitive types, or "stem reptiles," from which the later members of the class seem to have been evolved, are so like Amphibia that they might be classified with them (Fig. 452). The short limbs, extending laterally rather than vertically from the body, show that the body still rested directly upon the ground and that the limbs must have been used in the fashion of the amphibian. The diversification of reptiles began in the Permian; and, as the Amphibia declined, the Reptilia became the predominant land animals during the Mesozoic or Age of Reptiles. Among the lines that flourished and became extinct with the rise of the Mammalia in later times were the *dinosaurs*, the most diversified group of land vertebrates that has ever lived (Fig. 453 Below, and Fig. 473, p. 652); the *ichthyosaurs* and others which took to the water (Fig. 477, p. 655); the *pterosaurs*, which were flying reptiles distinct from the line giving rise to birds (Fig. 453 Above); reptiles ancestral to birds (Fig. 458); and those ancestral to mammals (Fig. 452 Above). Existing reptiles are remnants of a mighty race living in the days when dinosaurs commanded the land, ichthyosaurs the water, and pterosaurs the air. We can only guess at the factors involved in the decline of such a group. The reptiles flourished as animals that were obviously better suited to life on the land than amphibians, and the land was then occupied by no other large animals. Perhaps cold-bloodedness and brains smaller than the lumbar enlargements of their spinal cords were important in the decline of reptiles when the Age of Mammals began.

Among living reptiles, the members of the Order *Chelonia*, or turtles and tortoises, represent the most primitive type, although superficially they may seem the most specialized (Fig. 454 and Fig. 149, p. 230). The box-tortoise, *Terrapene carolina*, and the painted tortoise, *Chrysemys marginata*, are familiar examples. *Chrysemys marginata* and, more particularly, the soft-shelled tortoise, *Amyda spinifer*, illustrate the shift from land to water that has occurred in so many types

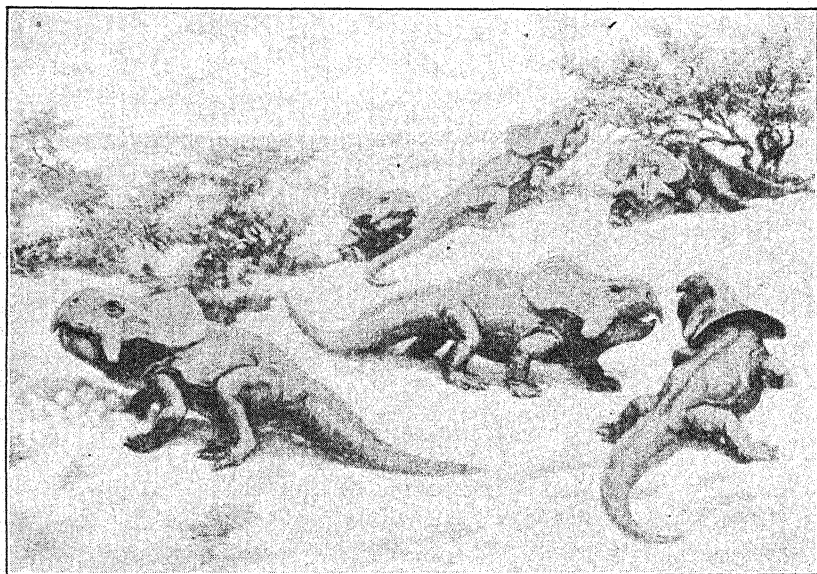
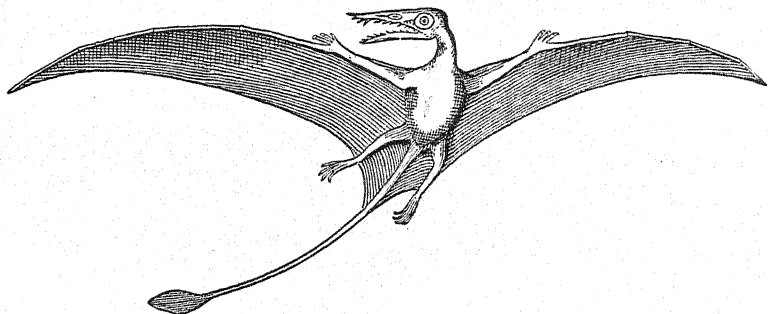


FIG. 453. Dominant reptiles of the past. *Above*, reconstruction of a flying reptile, the pterosaur, *Rhamphorhynchus phyllurus*, by Marsh. *Below*, reconstruction of the egg-laying dinosaur, *Protoceratops andrewsi*, and its eggs (cf. Fig. 474, p. 653).

(*Above*, redrawn from the figure by Marsh. *Below*, from the mural painting by Charles R. Knight, copyright by Field Museum of Natural History, Chicago; courtesy of the Museum.)

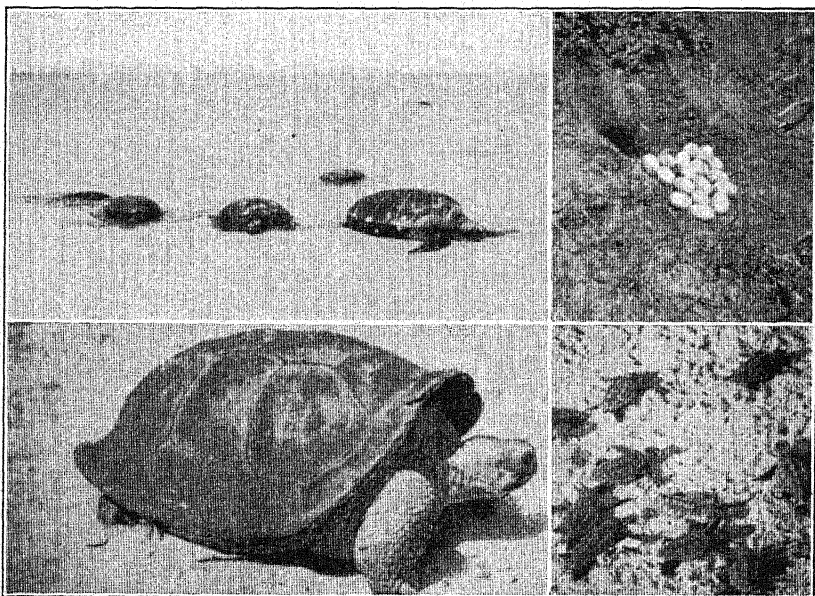


FIG. 454. Turtles, tortoises, and the egg-laying of reptiles. *Above*, nest and eggs of the Florida alligator, *Alligator mississippiensis*; the nest is usually made of flags and other vegetation scraped together in a low mound. The eggs are covered and warmed only by the sun's heat, although the female apparently remains in the vicinity until the juvenile alligators are hatched; the nest has been opened to show the eggs. *Middle-left*, green turtles, *Chelone mydas*, coming ashore for egg-laying. *Middle-right*, eggs and burrow of the Murray tortoise, *Emydura macquariei*. *Below-left*, the giant tortoise, of the Galápagos Islands. *Below-right*, young loggerhead turtles, *Caretta caretta*, making for the sea after hatching.

(*Above*, from A. M. Reese, "The alligator and its allies," copyright, 1915, by G. P. Putnam's Sons, reprinted by permission. *Middle-left and right*, from Charles Barrett, 1924, *Natural History*, vol. 24. *Below-left*, from F. A. Lucas, 1922, *Natural History*, vol. 22. *Below-right*, from G. K. Noble, 1930, *Natural History*, vol. 30. All by courtesy of American Museum of Natural History.)

of reptiles since their original adaptation for terrestrial life. The Chelonia are fundamentally air-breathing land animals, but some of them, such as the fresh-water and the marine species, have come to live

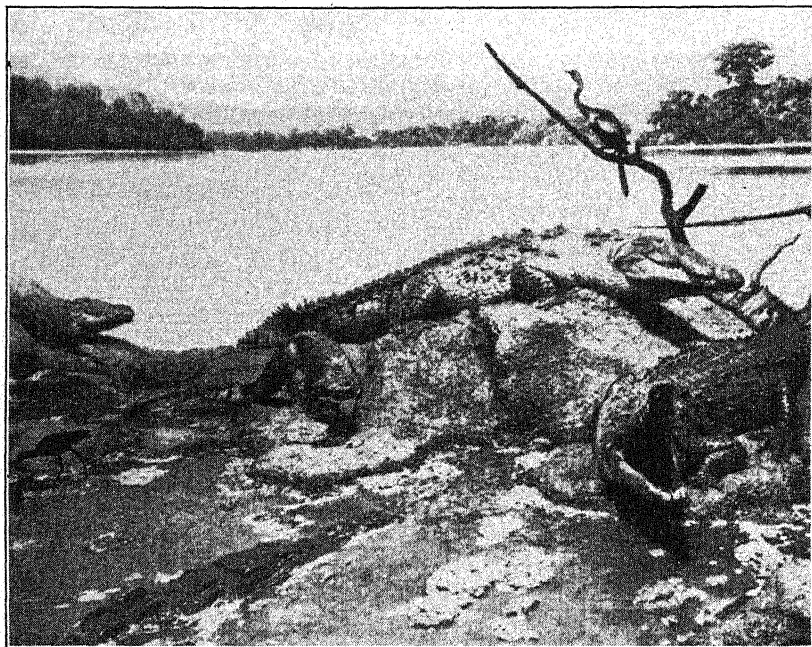
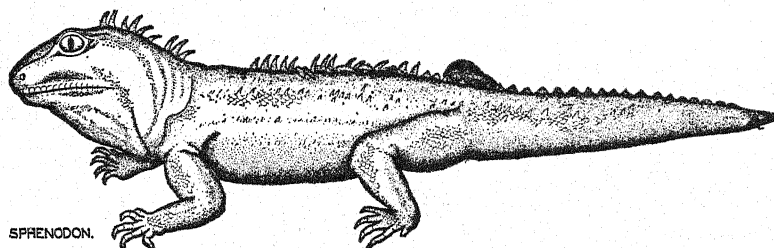


FIG. 455. Some existing reptiles. *Above*, *Sphenodon*, the single living genus of the Order Rhynchocephalia, which is a very primitive type. *Below*, the South American crocodile, *Crocodylus acutus*.

(*Above*, from Neal and Rand, "Comparative anatomy," copyright, 1936, by P. Blakiston's Son and Co., reprinted by permission. *Below*, photograph of group in Field Museum of Natural History, Chicago; courtesy of the Museum.)

partly in the water. These forms still breathe air and still come to land for their egg-laying. The extinct ichthyosaurs, plesiosaurs, and mosasaurs were evidently reptiles that lived in a similar fashion and presumably laid their eggs on land, as the dinosaurs seem to have done

(Fig. 453 Below and Fig. 474, p. 653). An extreme development of size among existing forms is seen in the giant tortoise of the Galápagos

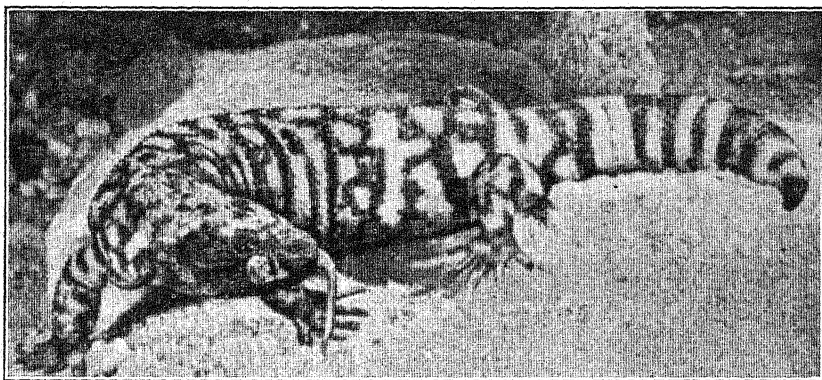


FIG. 456. Representative lizards. *Above*, the Gila monster, *Heloderma suspectum*, the only poisonous lizard, with one of the smaller lizards upon which it commonly feeds. *Below-left*, head of an iguana, a large lizard, illustrating the reptilian face. *Below-right*, giant lizard, *Varanus komodoensis*, of Komodo Island.

(*Above*, Museum photograph. *Below-left*, from Natural History, vol. 36. *Below-right*, Museum photograph. All by courtesy of American Museum of Natural History.)

Islands and in the large marine turtles, but these are dwarfs by comparison with some of the extinct chelonians.

A lone survivor of another primitive type, the Order *Rhynchocephalia*, is the Genus *Sphenodon* (Fig. 455 Above), now found only in

New Zealand. *Sphenodon* is of great importance to the comparative anatomist because it represents a very generalized and so a primitive type of reptile. It is more closely related to the lizards and snakes than to other familiar forms.

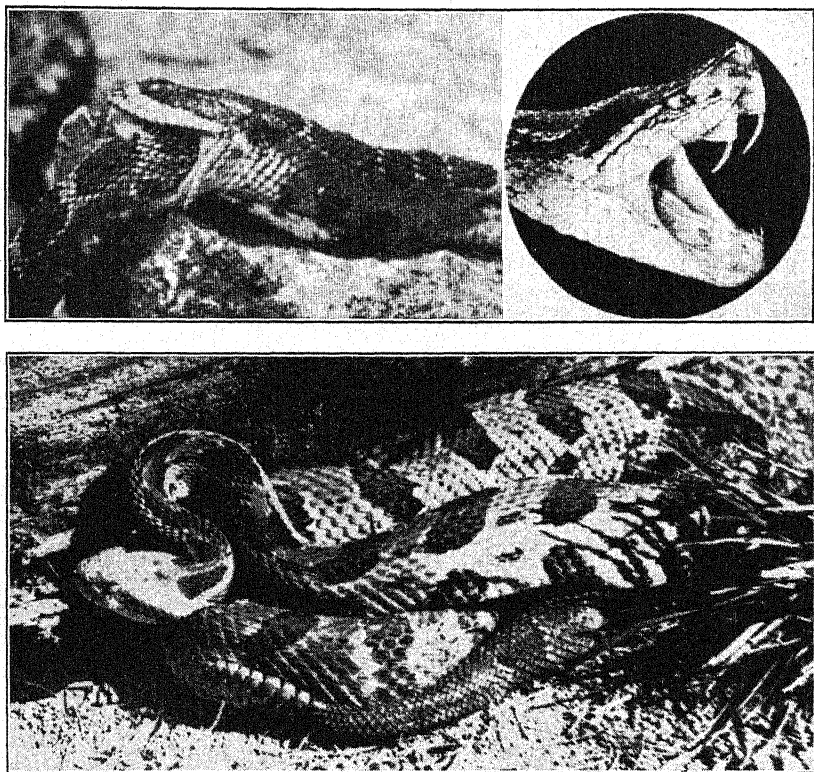


FIG. 457. Poisonous snakes. *Above-left*, a rattlesnake devouring another rattler. *Above-right*, fangs of the "fer de lance," *Bothrops atrox*, the most dangerous snake in tropical America. *Below*, a rattlesnake at home.

(*Above-left*, from H. L. Davis, 1937, *Natural History*, vol. 39; courtesy of American Museum of Natural History. *Above-right*, from B. Hathcock, 1937, *Natural History*, vol. 39; courtesy of American Museum of Natural History. *Below*, from photograph by Charles Schwartz.)

The lizards (*Lacertilia*, Fig. 456) and the snakes (*Ophidia*, Fig. 457) are so closely related that they are placed together in the Order *Squamata*. It appears from the fossil record that snakes are a comparatively recent offshoot from four-footed ancestors within this order. There are also a few limbless lizards now living that resemble snakes but have had an independent and more recent origin. The

various species of lizards in the warmer parts of the United States are familiar examples of the Lacertilia. The "horned toad," *Phrynosoma cornutum*, is a lizard, specialized by dorso-ventral flattening of the body, which presents somewhat the shape of a toad instead of the elongated outline seen in most lizards. The giant lizard, *Varanus komodoensis*, of Komodo (Fig. 456 Below, Right), which is one of the largest of existing reptiles, reaches a length of 10 feet and a weight of 250 pounds. It is a swift runner and a good swimmer, capturing large animals such as pigs and deer or feeding upon carrion as the opportunity is presented. The Gila monster, *Heloderma suspectum* (Fig. 456 Above), of the Arizona and New Mexico deserts is the only known lizard with *poison glands*. The chameleons are lizards that have unusual powers of changing color in relation to background, after the manner of many fishes and some amphibians. Many of the common lizards have this ability to a lesser degree.

The snakes are a very specialized although recent type (Fig. 457). In most genera the limbs have disappeared, but in a few, such as the pythons, minute vestiges are visible externally. Modifications of the ribs and vertebræ adapt the body for its lateral coiling and locomotion by pushing and bracing; the jaws and related bones are modified in such a manner that the mouth can be stretched surprisingly in feeding. The viscera are also greatly modified in connection with the elongation of the body. The *fangs* of poisonous snakes, such as the rattlesnake, are modified teeth associated with glands by which the *venom* is secreted. In contrast with this means of defense and offense, the boas and pythons, which are non-poisonous, attain great size and overpower their prey by using the head as a battering ram and then crushing the prey with their coils, as do some of the smaller snakes. The great majority of our common snakes are quite harmless, and such species as the bull snake render great service to man by their destruction of rodents, although they take a toll of the eggs and young of birds. Most species of lizards and snakes are *oviparous* in the manner typical for the Reptilia. A few species, such as the water snake, *Natrix sipedon*, have become *ovoviviparous*.

The Order *Crocodylia*, which includes the alligators and crocodiles (Fig. 455 Below), is represented in North America by the alligator. Here again are reptiles that have taken to the water, although still breathing air and coming to land for egg-laying (Fig. 454 Above), as well as living a land-and-water existence. In body shape the *Crocodylia* represent a generalized type, but part of the internal structure is much specialized, notably the brain, which is more highly developed than that of any other reptile. Early representatives of the

order were contemporaneous with dinosaurs and descended from the same stem among the primitive Reptilia.

The Aves. A bird can be defined as an animal with *feathers*, since these are distinctive. Otherwise, the birds are *warm-blooded* vertebrates closely resembling reptiles, from which it is clear they arose (Fig. 458). Among the earliest reptiles one line, from which the

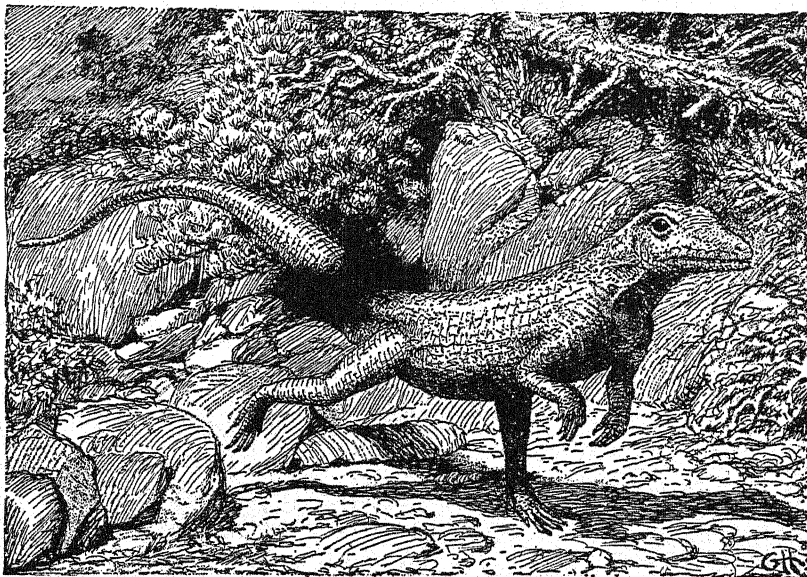


FIG. 458. Restoration of *Ornithosuchus*, a running pre-avian reptile.

(From Hellmann, "The Origin of birds," reprinted by permission of D. Appleton-Century Co., publishers.)

dinosaurs and the pterosaurs originated, was ancestral also to the crocodiles and to the birds. Toward the end of the Paleozoic or the beginning of the Mesozoic it is probable that small reptiles of this group, already specialized for locomotion with the hind limbs, were further modified for an arboreal habitat and flight. Whether the *wings* involved only the anterior pair of limbs at the outset or both pairs of limbs, as in the flying squirrels, is a matter of dispute among paleontologists. What is certain from the records is that birds came from reptiles and that the earliest known birds, *Archæopteryx* (Fig. 484, p. 663) and *Archæornis*, found in the Jurassic, had feathers and presumably a moderate power of flight, while still possessing obvious reptilian characters, such as teeth, that have been lost by the modern representatives of the class. No other fossils of birds are known until

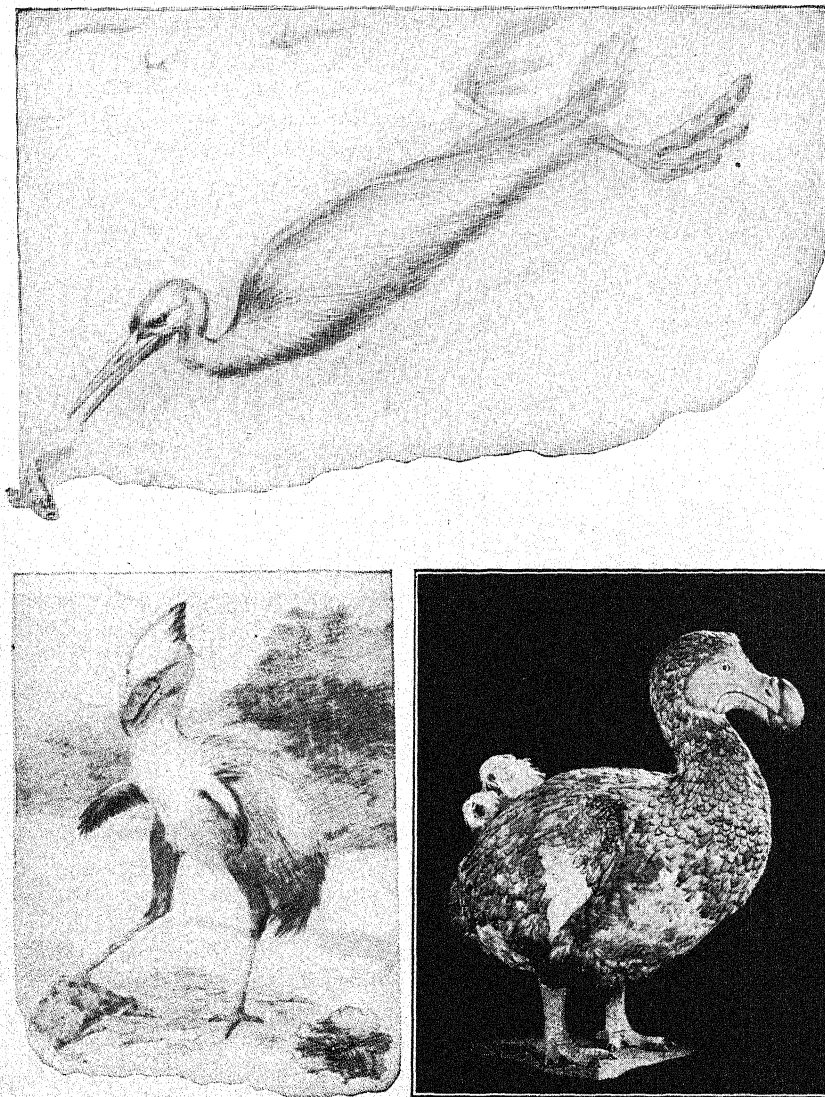


FIG. 459. Restorations of some extinct flightless birds. *Above*, *Hesperornis*, a wingless diving bird. *Below-left*, *Phororachus*, a gigantic running form with reduced wings. *Below-right*, the dodo, *Didus ineptus*, a large bird found on the island Mauritius; the last individuals were killed about 1700.

(*Above* and *below-left*, from Lucas, "Animals of the past." *Below-right*, from D. L. Edwards, 1935, *Natural History*, vol. 35. All by courtesy of American Museum of Natural History.)

the upper Cretaceous when the toothed aquatic forms *Hesperornis* (Fig. 459 Above) and *Ichthyornis* are found as lines that became extinct. It is assumed that birds were abundant in the upper Cretaceous, because the birds of the early Tertiary are diversified and essentially like those of today. In these modern forms the most important divergence in type is between the *flightless birds*, such as the existing

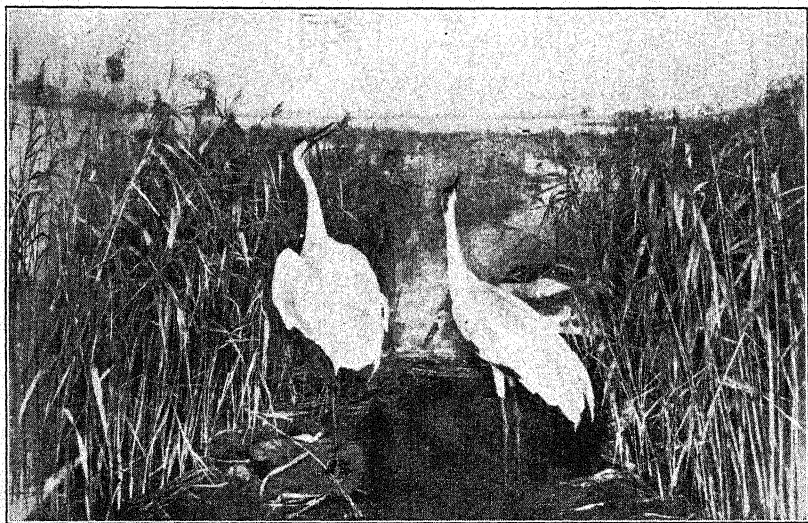
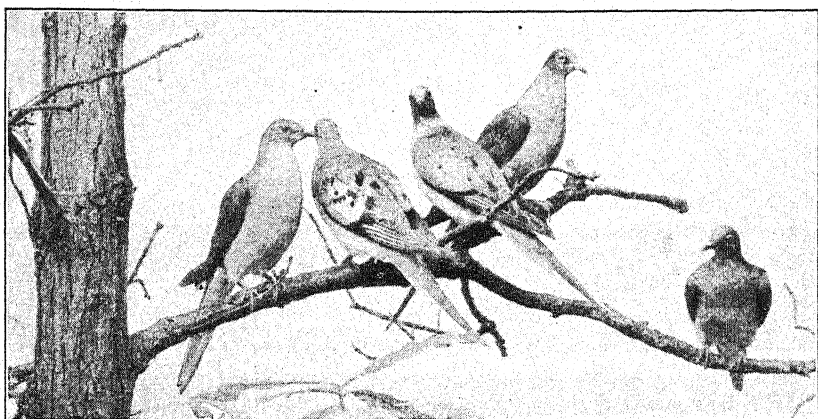


FIG. 460. Representative types of birds. *Above*, the passenger pigeon, originally present in countless numbers in North America but now extinct. *Below*, the whooping crane, barely saved from extinction in recent years.

(*Above*, from photograph of group in Field Museum of Natural History, Chicago; courtesy of the Museum. *Below*, from photograph of group in American Museum of Natural History; courtesy of the Museum.)

emus, kiwis, and ostriches, and the great majority of existing forms which are adapted for flight and have typically the *keeled sternum* for attachment of the powerful wing muscles as seen in the breastbone of a fowl. The poverty of the fossil record seems explicable by the fact that a bird with its lighter body, particularly its lighter bones, is much less likely to leave a record as a fossil than is a heavier animal. More fossils of birds may be discovered at any time, but it is improbable that the record can ever approach that of animals more commonly buried in the mud of some shallow body of water and thus fossilized. The relationships between the extinct types and the principal existing types of birds are shown by the classification that follows.

Class *Aves*

Subclass *Archæornithes*

Earliest known birds, forms with teeth and other reptilian characters. The extinct *Archæopteryx* and *Archæornis* (Fig. 484, p. 663).

Subclass *Neornithes*

Superorder *Odontognathæ*

Aquatic, toothed birds. The extinct *Hesperornis* (Fig. 459 Above) and *Ichthyornis*.

Superorder *Palæognathæ*

Various flightless birds, existing or recently extinct. The emus, cassowaries, kiwis, ostriches, rheas, moas, dodo, etc. (Fig. 459 Below).

Superorder *Impennes*

Penguins.

Superorder *Neognathæ*

All the more common and familiar birds, including the great majority of existing species (Figs. 460 and 461).

It will be recalled that another group of flying reptiles, the pterosaurs or pterodactyls (Fig. 453 Above) flourished and then became extinct. They were contemporaneous with the primitive birds and from the same reptilian line, although representing an independent offshoot. Characteristics probably advantageous to the birds were their warm-bloodedness, their nesting habit, the greater care given the young, and their feathers, which formed a strong, light, and insulating covering for the body. In a little volume entitled "This simian race," Clarence Day has considered the extent to which man is man because he arose from simians and not from carnivores or some other mammalian type. The birds represent a type that might have become dominant upon land instead of the mammals; they might even have evolved a level of intelligence comparable with that of man. One might speculate as to what such an "*Avis sapiens*" might have been like had the factors of evolution brought forth such a species instead of *Homo sapiens*.

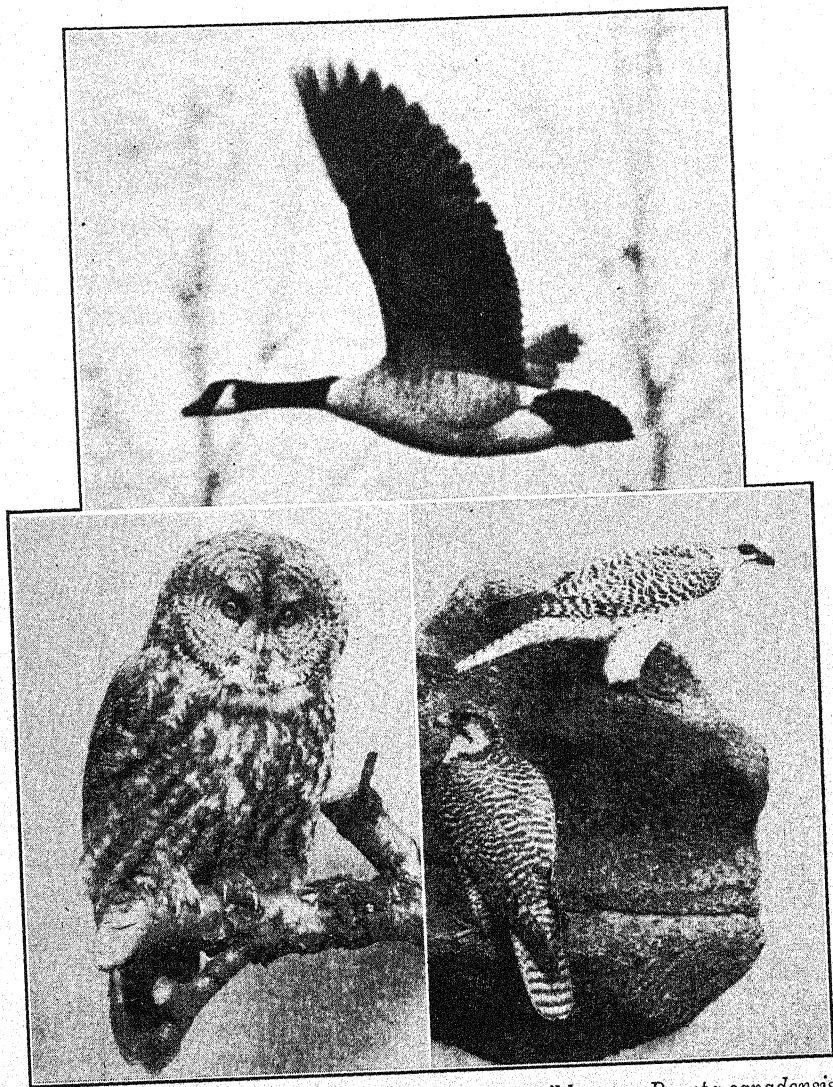


FIG. 461. Representative types of birds. Above, wild goose, *Branta canadensis*, in flight. Below-left, the great gray owl, *Scotiaptex nebulosa*, a nocturnal bird of prey. Below-right, gyrfalcons, *Falco islandus*, and *F. obsoletus*, typical birds of prey.

(Above, photograph by Charles Schwartz. Below-left and right, photographs of mounted specimens in Field Museum of Natural History, Chicago; courtesy of the Museum.)

A review of existing birds is impossible within the limits of this chapter (*cf.* Figs. 460 and 461). Despite diversity in appearance and habits they are a very unified group, as compared with such groups as the reptiles, living and extinct, and the mammals. The flightless birds of the present and recent times seem to have originated from flying ancestors, in relation to isolation in such places as Australia, New Zealand, and Madagascar, where there were few if any carnivorous enemies, and not from ancestors in which the power of flight had never developed. Apparently flight has been lost in a number of independent lines during the evolution of the class (Fig. 459). Many recent birds have become modified in relation to aquatic feeding, although none so completely as the penguins. Most characteristic of existing bird life are the small perching birds familiar as our common songsters.

The Mammalia. A mammal might be loosely defined as a reptile further specialized for terrestrial life. Mammals can be defined technically as animals with *hair* and *mammary glands*, without specifying the less obvious characters by which they may be further distinguished. In intelligence they are the highest class of vertebrates, and one thinks of them as highest in complexity of structure, although birds and mammals alike represent a climax in specialization. The characteristics by which mammals are better qualified than reptiles for terrestrial life are their *warm-bloodedness*, their manner of *reproduction*, their mechanism of *locomotion*, and, by no means least, their *brains*. To a lesser extent their ears, eyes, and teeth seem more efficient than those of reptiles. The comparison presents the mammal as an animal more capable of going into action, maintaining action, and reproducing its kind than any of its reptilian ancestors or contemporaries. The major subdivisions of the Mammalia are as follows:

Class *Mammalia*

Subclass *Prototheria*

The oviparous, or egg-laying, mammals. The duckbill, *Ornithorhynchus*, and the spiny ant-eater, *Echidna* (Fig. 462).

Subclass *Metatheria*

The marsupial, or pouched, mammals. The dasyures, bandicoots, and opossums (Fig. 462), and the wombats, phalangers, and kangaroos.

Subclass *Eutheria*

The viviparous mammals, which include all the more familiar mammals (*cf.* Figs. 463-468). The orders of the Eutheria are as follows:

Order *Insectivora*. The moles, shrews, and hedgehogs.

Order *Chiroptera*. The bats.

Order *Dermoptera*. The flying lemurs.

Order *Primates*. The lemurs, monkeys, apes, and man.

- Order *Carnivora*. The carnivorous mammals, such as the cats, lions, tigers, leopards, dogs, wolves, civets, foxes, hyenas, raccoons, bears, otters, and weasels; and the seals, sea-lions, and walruses.
- Order *Perissodactyla*. The odd-toed hoofed mammals, such as the horses, asses, zebras, tapirs, and rhinoceroses.
- Order *Artiodactyla*. The even-toed hoofed mammals, such as the pigs, peccaries, hippopotamuses, camels, llamas, alpacas, deer, antelopes, cattle, sheep, goats, and giraffes.
- Order *Cetacea*. The whales, dolphins, and porpoises.
- Order *Proboscidea*. The elephants.
- Order *Sirenia*. The sea-cows (*cf.* manatee, Fig. 463).
- Order *Hyracoidea*. The coneys.
- Order *Rodentia*. The rodents, such as, the squirrels, prairie dogs, beavers, rats, mice, guinea-pigs, porcupines, and rabbits.
- Order *Xenarthra*. The sloths, armadillos, and ant-eaters.
- Order *Pholidota*. The pangolins, or scaly ant-eaters.
- Order *Tubulidentata*. The aardvark.

The three Subclasses *Prototheria*, *Metatheria*, and *Eutheria*, represented by the duckbill, the opossum, and the more common mammals, respectively, and also the nature of mammalian development should be kept in mind throughout the account that follows. There is clear evidence from the fossils of the mammalian beginnings. Reptiles along the line toward mammals are found in the Carboniferous and Permian of Texas; forms even more like mammals occur in the Permian and Triassic of South Africa, where they were the most common of all reptiles. Their mode of development not being known, some of these forms, such as *Cynognathus* (Fig. 452 Above), might as well be called mammals as reptiles. If it were known that they had given up the egg-laying habit, they would certainly be called mammals. Although no one genus among these fossils can be fixed as the specific ancestor, it appears that in the African region a type of reptile gradually became modified so that it walked with its limbs more beneath the body, and hence with the body off the ground; and from such members of the reptilian stock the mammals arose. One outcome of this change that may have been important was the ultimate possibility of more rapid locomotion.

How and when these animals became *warm-blooded*, *hairy*, and *viviparous* are matters of speculation. It has been suggested that increasing dryness of the climate and so a drier land surface, for which there is evidence in the geologic records of the period, may have been factors of importance in determining the types that survived. These reptile-mammals became extinct with the rise of the reptiles in the Mesozoic, but they seem to have left descendants that were truly mammals and contemporaneous with the dinosaurs. Small forms of this sort,

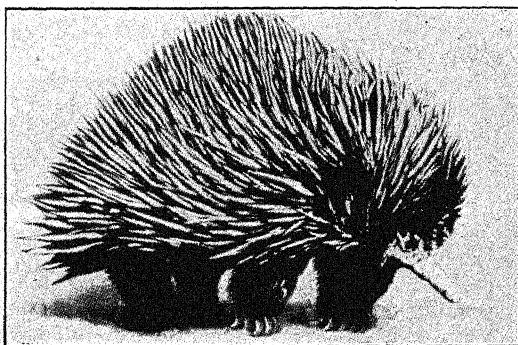


FIG. 462. Primitive types among existing mammals. Above, the duckbill, *Ornithorhynchus anatinus*. Middle-left, the spiny ant-eater, *Echidna aculeata*. Below-left, an opossum, *Didelphys virginiana*, and her young. Below-right, the same individual with the young at an earlier stage within the pouch.

(Above, from T. J. Parker and W. A. Haswell, "Textbook of zoölogy," copyright, 1921, by Macmillan and Co., Ltd., reprinted by permission. Middle-left, from W. Stempell, "Zoölogie im Grundriss," 1926. Below-left and right, from photographs by Charles Schwartz.)

not larger than a rat, are known from fragmentary remains sparsely distributed throughout the Mesozoic. The fossils are principally jaws and teeth; not a single complete skeleton has been discovered and not even a complete skull until a time near the end of the Age of Reptiles. To judge from their teeth some of these mammals seem to have been insect-eaters, a feeding habit that would include other small animals in addition to insects; others had teeth like those of plant-eaters. It appears from a variety of evidence that they were arboreal; they may have been nocturnal like many small mammals today. With the reptiles so diversified and occupying the land, the water, and the air, there remained perhaps a greater degree of safety in the arboreal habitat. In any event small mammals are found early in the Mesozoic, and they seem to have remained much as they were until the diversification of the Eutheria, or placental mammals, began near the end of this period.

Evolutionary changes have taken place not only in the adult structure of the mammals, as compared with reptiles, but also in their embryonic stages. The reptilian ancestors probably laid eggs as do modern reptiles (Figs. 453 and 454). The Prototheria, as represented by the duckbill and the spiny ant-eater (Fig. 462), lay eggs somewhat resembling those of reptiles. The Metatheria, such as the kangaroos and opossums (Fig. 462), bring forth relatively undeveloped young, which are carried in the pouch or marsupium. In the Eutheria the young are attached to the mother's uterus by the placenta and so nourished until they are born in more advanced stages, ranging from blind and hairless mice to colts that stand and run within a short time after birth. The Metatheria may be regarded as survivors of an evolutionary stage intermediate between the egg-laying ancestors and the placental mammals, although they are not ancestral to these mammals. Study of mammalian in comparison with reptilian embryos shows that the embryonic membranes of the mammal so closely resemble those of the reptile and bird that they must have been derived from the reptilian source. There is no yolk in the mammal's egg, but there is an empty yolk sac (*cf.* Figs. 91 and 93, pp. 151 and 153).

Thus, mammals of small size were present as an insignificant fraction of the population during the millions of years that witnessed the rise and dominance of the dinosaurs and other ruling reptiles and the rise of the birds. The fossil record is incomplete; but, if there had been many larger species of mammals, some would certainly have been preserved as fossils and found before this. Only toward the close of the Mesozoic, which marks the end of the Age of Reptiles, did the diversification of the mammals begin. In the Age of Mammals, when this class of warm-

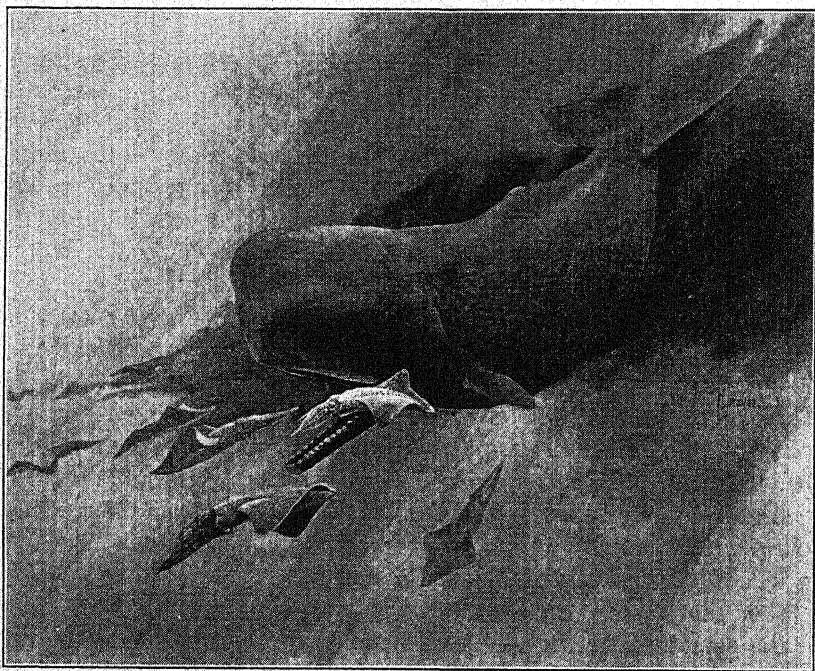
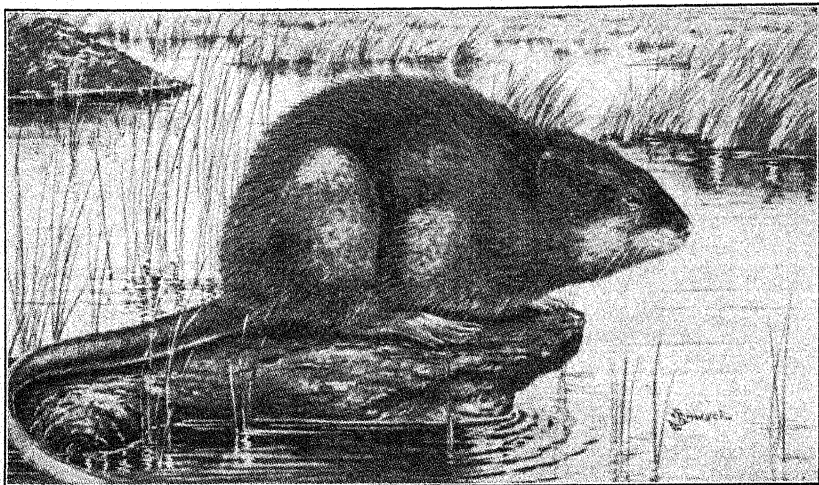


FIG. 463. Mammals that have taken to the water. *Above*, the muskrat, *Ondatra zibethica*, in its haunts. *Below*, sperm whale, *Physeter macrocephalus*, feeding upon squids (*Continued*, p. 635).

(*Above*, from N. Hollister, 1911, "Systematic synopsis of the muskrats," North American Fauna, No. 33, Bureau of Biological Survey U. S. D. A. *Below*, from R. C. Murphy, 1933, Natural History, vol. 33; courtesy of American Museum of Natural History.)

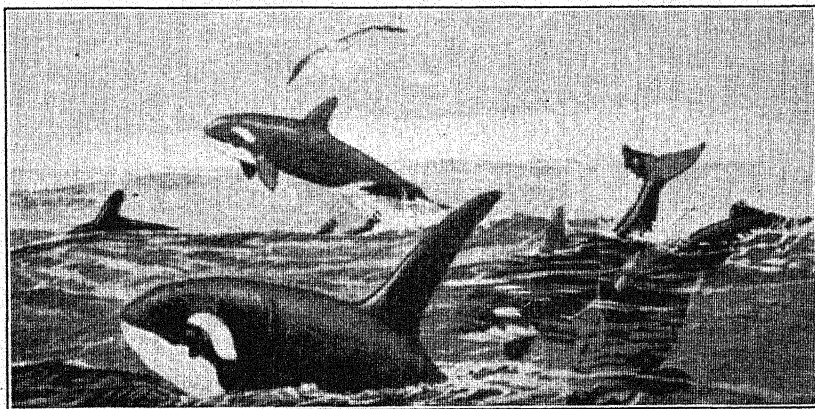
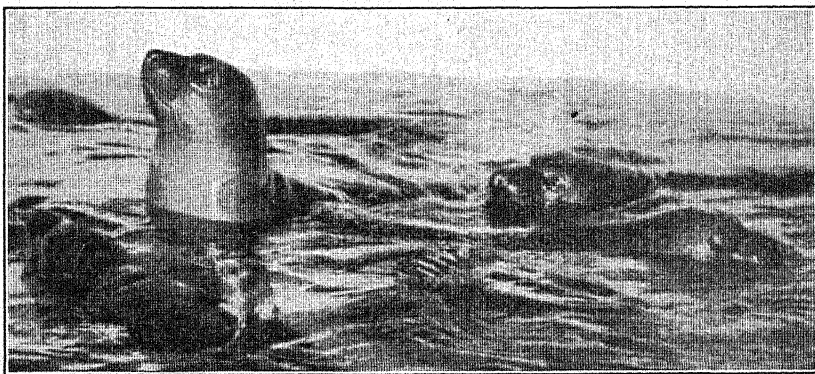


FIG. 463. Mammals that have taken to the water (*Concluded*). Above, the manatee, *Trichechus latirostris*, one of the sea-cows. Middle, yearling elephant seals, *Mirounga*, in an aquarium. Below, killer whales, *Orca orca*.

(Above, from painting by Charles R. Knight. Middle, from C. H. Townsend, 1924, *Natural History*, vol. 24. Below, from J. T. Nichols, 1929, *Natural History*, vol. 29. All by courtesy of American Museum of Natural History.)

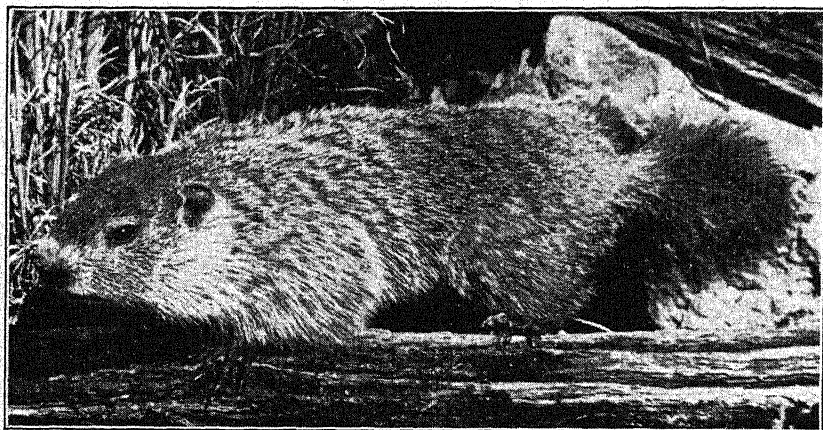
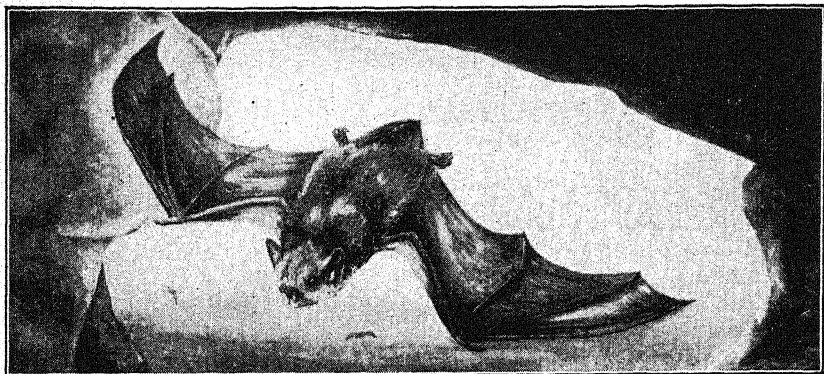


FIG. 464. Mammals of the air, ground, and trees. *Above*, a bat, *Myotis*, entering its cave. *Middle*, a woodchuck, *Marmota monax*, near its den. *Below*, a "treed" raccoon, *Procyon lotor*.

(*Above*, from mural painting by Charles Schwartz. *Middle* and *Below*, from photographs by Charles Schwartz.)

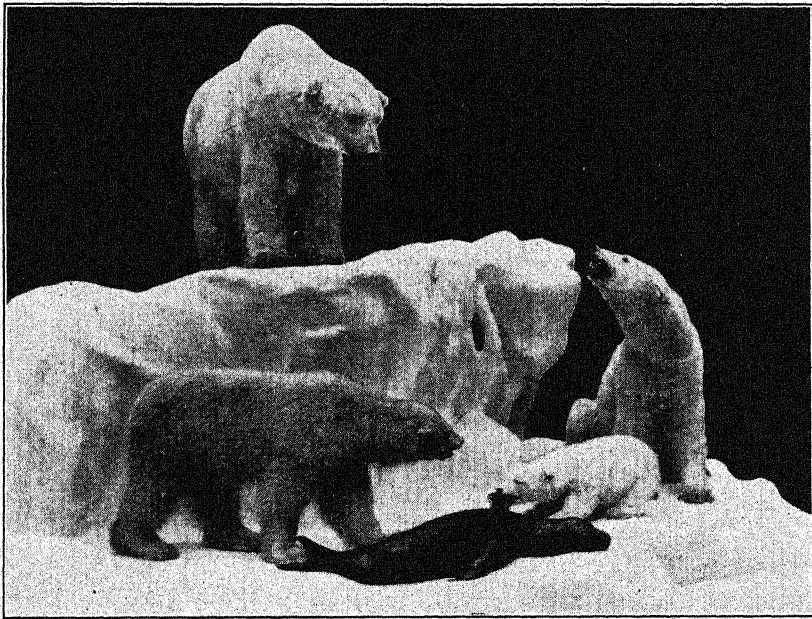
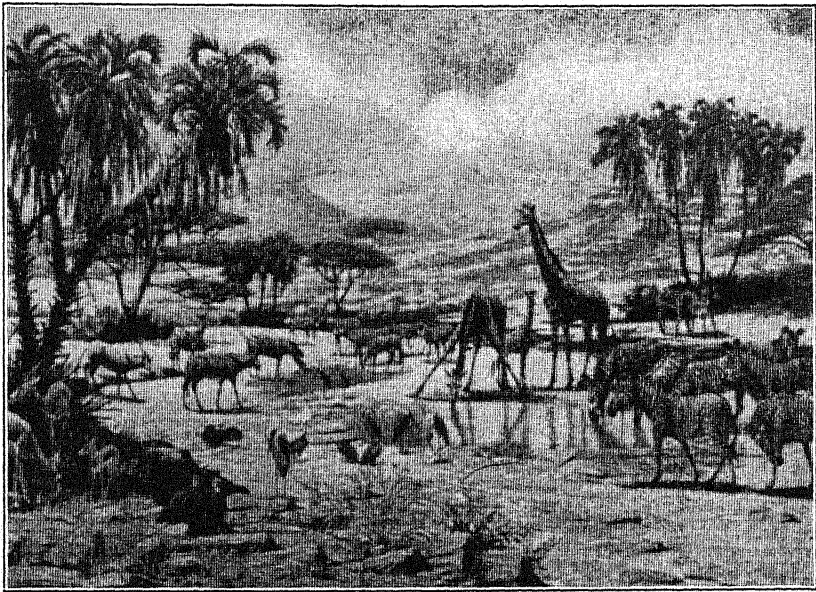
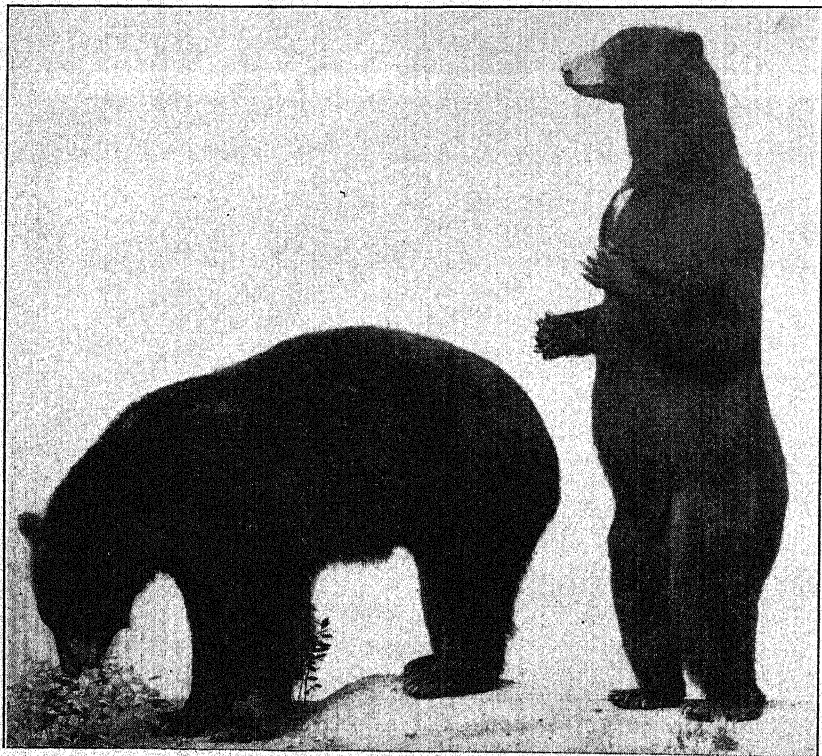
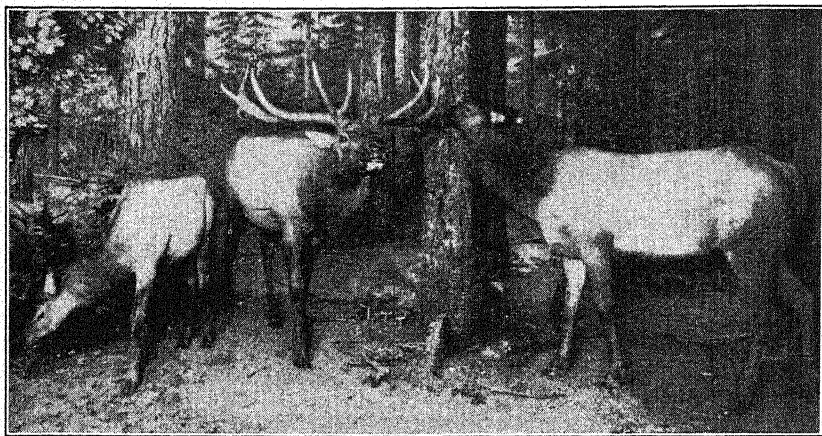


FIG. 465. Mammals of the tropics and the polar regions. *Above*, zebra, giraffe, oryx, marabou stork, and other African animals at a water hole. *Below*, polar bear group with captured seal.

(*Above*, from A. R. Dugmore, 1932, *Natural History*, vol. 32; courtesy of American Museum of Natural History. *Below*, from group in Field Museum of Natural History, Chicago; courtesy of the Museum.)



• FIG. 466. Mammals of the forest. Above, the Olympic elk, or wapiti, *Cervus canadensis*. Below, the American black bear, *Euarctos americanus*.
(From groups in Field Museum of Natural History, Chicago; courtesy of the Museum.)

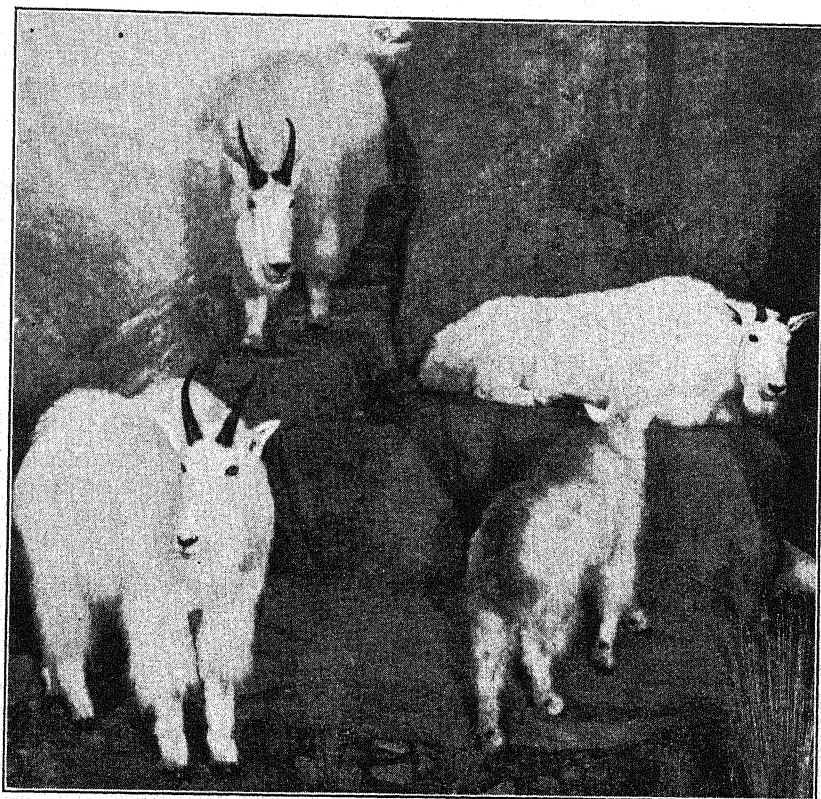


FIG. 467. Mammals of the heights. *Above*, Rocky Mountain goats, *Oreamnos americanus*. *Below*, Marco Polo's sheep, *Ovis poli*.

(From groups in Field Museum of Natural History, Chicago; courtesy of the Museum.)

blooded vertebrates became dominant upon the land, mammals seem to have replaced reptiles by an expansion into territory that was being relinquished. The mammals were the more efficient of the two; they

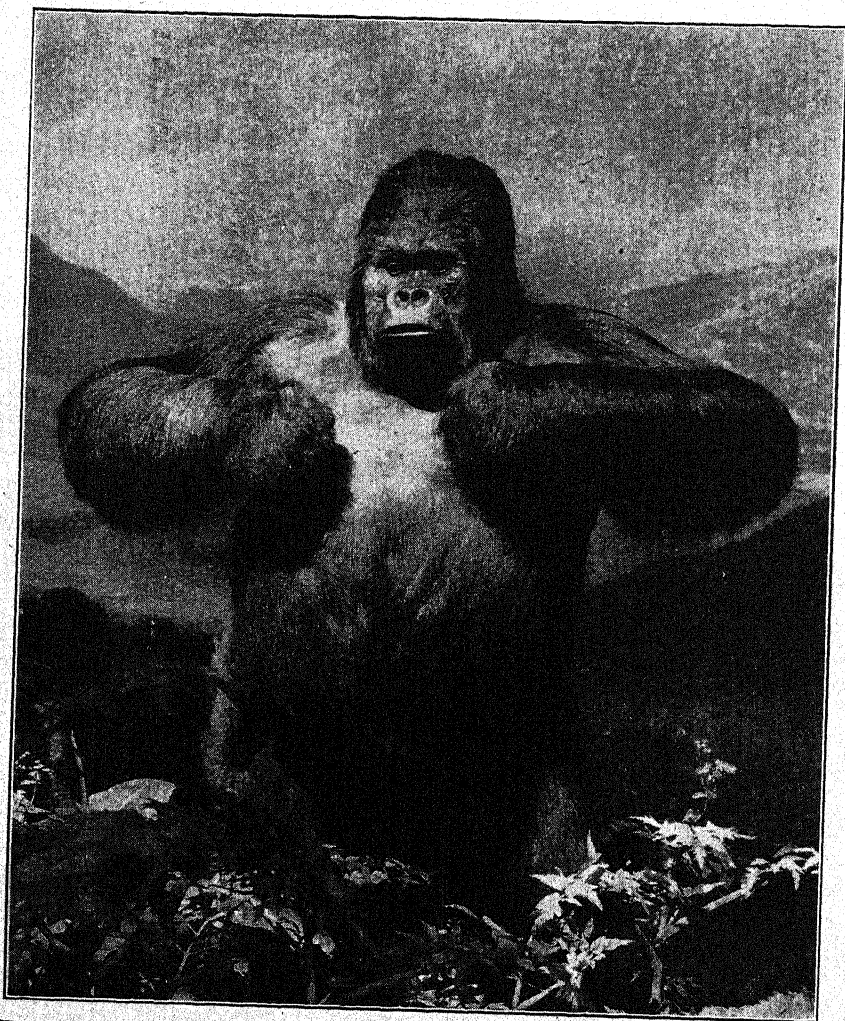


FIG. 468. Male gorilla, *Gorilla beringei*, from Mt. Karisimbi region in Africa. (From the mounted group in American Museum of Natural History; courtesy of the Museum.)

had warm blood, which enabled them to range at will, and greater possibilities of locomotion, to say nothing of wits. What seems to have happened is not that the more efficient type drove out the less efficient but that the reptiles declined for some unknown reason, and so the land

again became free for new occupants. The mammals were at hand and became the dominant land forms of the Tertiary, or Age of Mammals, as the early amphibians and reptiles had become dominant upon the older land surfaces. The early mammals were small insect-eaters, but diversification into the principal mammalian types was rapid, and with increase in size of the individuals in many lines the great mammalian fauna of the Tertiary came into being. Like the fishes, amphibians, and reptiles, the mammals had their day; they were a waning race even before many recent forms were confronted with ultimate extinction through the activities of *Homo sapiens*. Representative types of existing mammals are shown in Figs. 462-468.

Along with that of other mammals, the human line of descent begins with the insect-eaters of the trees at the close of the Age of Reptiles. Surviving offshoots that mark the path of this evolution are the existing lemurs, tarsiers, monkeys, and great apes (Fig. 468); this descent is confirmed by what is known from fossils (Fig. 493, p. 679). Only in the late Tertiary or earliest Pleistocene, it seems, did our ancestors descend from the trees; binocular vision and important qualities of hand and brain, along with the beginnings of an upright posture, were established before man's forebears came to earth. The later phases of human evolution are outlined in Chapter 20. Speaking of our ancestors in the early Tertiary, W. D. Matthew describes their appearance as intermediate between that of a lemur and a mongoose. They were animals "rather catholic in their tastes, living among and partly in the trees, with a sharp nose, bright eyes and a shrewd little brain behind them, looking out, if you will, from a perch among the branches, upon a world that was to be singularly kind to them and their descendants."

Summary

The Phylum Chordata includes certain invertebrate animals along with the familiar vertebrates. The species representing the lowly members of the phylum are few in number and superficially unlike their numerous vertebrate relatives. Yet they have the gill slits, notochord, and nervous system of the chordate. Since vertebrates appear as fishes in the Ordovician, it is concluded that these first vertebrates of the fossil record must have been preceded by fairly complex ancestors in the Cambrian, in which representatives of all the other major phyla are found. This means that a common ancestor for all chordates would be sought in the Age of Invertebrates. No fossils representing such an ancestor are available, and it is unlikely that any will ever be found. The origin of vertebrates from some invertebrate

source was the subject of much speculation, based upon the data of comparative anatomy and embryology, when such theorizing was the vogue in the last decades of the nineteenth century; nothing that proved convincing was ever made of the matter, and it is unlikely that anything ever will be. The animal life of the Cambrian is remote, but it was preceded by millions of years from which we have virtually no fossils and during which the Cambrian types were evolved. In studying evolutionary history within the Subphylum Vertebrata, we have access to the fossil record and also to "surviving fossils," such as the egg-laying mammals, whose structure and development can be fully examined. Reconstructing the past from the data available, we conclude that the earliest vertebrates were small, heavily armored, bottom-dwelling, fish-like animals, living in fresh rather than the salt water from which their ancestors presumably came. From such early fishes came others that made a beginning of air-breathing while still in fresh water, and some of these invaded the ocean. Late in this Age of Fishes came the first land vertebrates, as Amphibia descended from the air-breathing fishes known as lobe-fins. In the Age of Amphibians, when the great coal measures were being laid down, these vertebrates were the dominant forms upon the marshy land surface. Reptiles arose from early amphibians and succeeded them in the Age of Reptiles. The mammals appeared as an early offshoot from the reptilian line, but they remained small and insignificant animals until the reptiles began to decline. Birds also came from reptiles. In the Age of Mammals the members of this class were able to range more widely than any of their predecessors, because of their effective locomotion, their warm-bloodedness, and their mode of development within the parent. As the mammals declined toward the end of the Tertiary, the human stock became differentiated from other Primates; the present is sometimes called the Age of Man.

CHAPTER 20

THE EVOLUTION OF ANIMAL LIFE

Astronomy tells us that our sun and its planetary system have probably undergone changes through countless years, as other suns seem to be changing at the present day. Geology tells us that our planet, the earth, has had a long and varying history. Such processes of change, which are relatively gradual and continuous, are known as evolution. Evolution is a widespread phenomenon, of which the examples to be found in the study of astronomy are discussed as *cosmic evolution* and those illustrated by a study of geology as *geologic evolution*. These two subdivisions of evolution are sometimes grouped together as *inorganic evolution*. On the other hand, *organic evolution* is the historic process of change by which organisms have reached their present state. As we are primarily concerned with organic evolution, the discussion cannot be extended to the inorganic field. It will be understood, however, that evolution is the scientist's answer to the question of how the world about us—stars and planets, mountains and oceans, animals and plants—has reached its present form. Hence, evolution involves events that have no obvious beginning or end in time or space, since it includes the processes by which cosmic bodies, as well as living things, have come into existence and by which they will continue without much change, will evolve into some new state, or will become extinct.

The Origin of Life

Time of Origin. The period at which protoplasm appeared upon the earth must have been remote, since the age of fossil-bearing rocks is to be reckoned in hundreds of millions of years, and since the original organisms must have antedated any fossil remains by a considerable period (Fig. 469). There undoubtedly was a time when the earth was too hot to support anything resembling protoplasm as we know it today. Protoplasm probably appeared during the period between this heated state and the time of the earliest fossils, after suitable environ-

mental conditions had arisen. If the age of the Cambrian fossils is as great as some geologists now believe (Fig. 469), organisms may have come into existence some 2,000,000,000 years ago.¹ In arriving at such a conclusion one must have due regard for the limitations of all attempts to estimate geologic time. What can be said with certainty is that protoplasm has existed upon our planet for a very long period, as shown by the record in the rocks, and that it was presumably in existence for a long while before the time of the earliest fossils. In this connection it will be noted that the period during which the higher animals, such as the vertebrates, have been in existence is only a small fraction of the entire history of organisms.

Manner of Origin. Here again, one must have recourse to speculation based upon facts that suggest possibilities. According to the *Cosmozoic Theory*, the original protoplasm accidentally reached the earth from some other body in space. It can be supposed that the primeval organisms of our planet arose from such an original "infection," and that the vast array of plants and animals that have since existed have been evolved from this ancestry. This theory is unsatisfactory because it does not explain how the protoplasm originated, which is the real question at issue. The problem is sufficiently remote from any possible solution if the origin of life is traced to the early stages of the earth. It becomes hopeless if the origin is removed to some other body in space, since there still remains the question of how life could have come into existence in another part of the universe. Moreover, it may be objected that the infecting protoplasm could not have survived the low temperature of interstellar space, nor the heat generated by bodies entering the earth's atmosphere. The possibility that such a cosmic rain of protoplasm became the source of living things upon our planet has not appealed to many biologists.

Another theory of the origin of organisms upon the earth is that of *Miraculous Creation*. As a philosophical concept, one may suppose that the primeval protoplasm arose by some creative act which was miraculous in the sense that it was not part of the order of nature. Scientists can only say regarding this theory that there are no facts which are suggestive of such a process.

¹ Three methods have been used by geologists in estimating geologic time. One is based upon the rate of sediment formation and therefore the time necessary to form sedimentary rock. Another is based upon the time necessary to produce the present salinity of the ocean, assuming that the first oceans were not salt. The third, which seems far more accurate than either of the others, is based upon the rate of disintegration, into lead and helium, of radioactive minerals.

There remains what may be termed the *Naturalistic Theory*. Here, again, there is only suggestive evidence, although it is possible that facts may sometime be discovered that will lend more definite support. According to this hypothesis, when conditions became suitable, a relatively simple protoplasmic substance arose, having the properties of life although perhaps in a more elementary fashion than any living bodies that now exist. Such protoplasm, becoming more complex, may have formed the units now called cells. The division of labor between nucleus and cytosome, as it appears in the cell, would then be regarded as the first great step in the evolutionary changes whereby a relatively simple material having some of the properties of protoplasm became differentiated into organisms composed of cells and to that extent resembling organic life as we know them today. With cells in existence the origin of many-celled organisms from the primitive unicellular ancestors. According to this theory, the cell would not be the most primitive form of organization. Instead, cells would have arisen as a stage in the evolution from the primitive living stuff. If this speculation is followed a step farther, it may be supposed that the unicellular organisms of the present day have descended from such early cells without evolving beyond the unicellular state but with much specialization as single cells. The many-celled organisms have advanced beyond the primitive single-celled state with much specialization of cells for particular functions.

It is not necessary to present the speculations regarding the manner in which a union of organic materials to form a physico-chemical system having the characteristics of protoplasm might have occurred. These speculations are many and varied, and they are based upon what is known of the physico-chemical properties of protoplasm as it now exists. But certain facts of biological and of chemical science may be noted. In the first place, protoplasm is not known to originate by any such natural or spontaneous process; it comes only from pre-existing protoplasm. Up to the present day, all theories of spontaneous generation have failed to be substantiated (*cf.* p. 273). This fact does not support the theory that protoplasm could have been so produced in the past. There is, however, one way in which data corroborative of the Naturalistic Theory of the origin of life might be obtained. Long ago chemists began to synthesize organic compounds which had previously been obtainable only as synthesized by organisms. Today, there seems no reason why any compound may not be thus produced under laboratory conditions. Again, living things can still be distinguished from non-living bodies, but such studies as those upon the viruses (*cf.* p. 275) make this distinction not as clear as it has seemed. It is not unreason-

able to suppose that organic compounds may have been synthesized in nature under conditions that once existed upon the surface of the earth or in its primitive oceans. Such compounds can be produced in our laboratories today and hence may have been formed in the laboratory of nature. If the biochemists are ever able to produce a simple system









ERAS	PERIODS	DURATION IN YEARS	DOMINANT LIFE	CHARACTERISTIC LIFE
CENOZOIC	RECENT	10,000	Man	
	PLEISTOCENE	1,000,000		
	PLIOCENE	6,000,000		
	MIOCENE	12,000,000		
MESOZOIC	OLIGOCENE	16,000,000	Mammals	
	EOCENE	20,000,000		
	PALEOCENE	5,000,000		
	CRETACEOUS	65,000,000	Reptiles	
	JURASSIC	35,000,000		
	TRIASSIC	35,000,000		
PALEOZOIC	PERMIAN	25,000,000	Amphibians	
	CARBONIFEROUS	85,000,000		
	DEVONIAN	50,000,000	Fishes	
	SILURIAN	40,000,000		
	ORDOVICIAN	85,000,000	Invertebrates	
	CAMBRIAN	70,000,000		
PROTEROZOIC	UPPER PRECAMBRIAN	650,000,000	Primitive Multicellular Forms	
ARCHEOZOIC	LOWER PRECAMBRIAN	650,000,000	Unicellular Forms	 Magnified 300 Times

FIG. 469. The geologic succession.

(Courtesy of the American Museum of Natural History.)

constructed of organic and inorganic compounds and having the essential capacities of protoplasm, it will seem quite reasonable to suppose that protoplasm thus originated in the early history of our planet.

Place of Origin. It has usually been assumed that organisms existed first in water and hence in the primitive oceans. The seas were formed, according to the theories of geology, when the atmosphere began to be differentiated from the hydrosphere, or watery covering of the globe. Presumably, the first oceans were boiling hot, and the land was, at the same time, the scene of great volcanic action. For a long time protoplasm, as we know it, could not have existed. As cooling progressed and conditions became more favorable, the seas may have teemed with living things before the land surface became suitable for habitation. Certain facts of marine ecology suggest this inference.

Organic Evolution

Organic evolution is the history of living things as interpreted by the biologist. As with the interpretations of geologic history that were brought together by Lyell (Fig. 470), the conclusions regarding organic evolution are based upon facts immediately before us, such as the structure and development of animals, their distribution over the earth, the fossils in the rocks. Much confusion arises regarding organic evolution through failure to distinguish between the historic sequence of events, or what may be termed the fact of evolution, and the various factors that have conditioned, and so determined, evolutionary changes. This may be illustrated by an analogy. If an airplane has flown from New York City to San Francisco, one may distinguish between the fact that the plane followed a particular course and the factors that determined this course. First, there were the structure and the functioning of the plane itself. The wings, engines, and rudders were factors conditioning speed and altitude. Second, there were environmental factors which were no less important. A low cloud ceiling over the Alleghenies delayed the passage and changed the altitude at which the plane flew. A storm in the Ohio Valley resulted in a more northerly course. Favorable weather in the plains region enabled the plane to fly at an optimum altitude. Storms in the Rockies further affected the flight before the arrival at San Francisco. An observer might trace the course of such a flight and still know little concerning either the internal or external factors involved. So it is with evolution. One may have convincing evidence that animals have changed and that these evolutionary changes have followed particular courses, such as

the development from lobe-finned fishes to amphibians and thence to existing land vertebrates (*cf.* p. 602), or the evolution from five-toed ancestors to the present-day horses; but one may still question the factors in organism and environment that brought about this evolution. The facts and factors of evolution are thus separable, although closely related. In general it may be said that scientists consider organic evolution well established as a historic fact, whereas the condi-



FIG. 470. *Left*, Georges Cuvier (1769–1832), comparative anatomist and paleontologist. *Right*, Sir Charles Lyell (1797–1875), author of “*Principles of geology*” (1830), a book that established the fact of geologic evolution.

(*Left*, from W. A. Locy, “*Biology and its makers*,” copyright, 1908, by Henry Holt and Co., reprinted by permission; *right*, from L. V. Pirsson and C. Schuchert, “*Textbook of geology*,” John Wiley & Sons, copyright, 1924, reprinted by permission.)

tioning factors of such evolution, whether internal or environmental, have not been ascertained, although progress has been made in their disclosure.

The evidence suggesting that unicellular organisms were the ancestors of the present multicellular plants and animals has been noted in earlier chapters (*cf.* pp. 232 and 295). The facts of comparative anatomy and embryology suggest further that such acquisitions as a gut cavity, some type of body cavity, and bilateral symmetry were important steps in the early evolution of the more complex types of animals. Figure 135, p. 215, represents a genealogical tree of these steps in evolution as well as a system of classification. To postulate such broad steps in evolutionary change takes us far back of the earliest fossils, and the evidence is suggestive rather than conclusive. Within the phyla that have left a considerable record as fossils, the evidence

is much more definite, as is shown by the special examples that will be cited in the succeeding sections of the present chapter.

Another aspect of the course of development within the phyla is the evolution of animals with respect to their habitats. The ocean seems to have been the original home of all the major phyla, but throughout their history some members of every system have tended toward fresh water and the land; and it also happens that, after becoming established upon the land, some forms have returned to the water. Thus, in the sponges and coelenterates the majority are marine, but a few species occur in fresh water. In the flatworms there are abundant marine and fresh-water turbellarians, and a few turbellarians are found upon the land. The annelids include marine and fresh-water species and also the earthworms. The more primitive mollusks are marine, but there are many species in fresh water and many upon the land, some of those in fresh water being perhaps descended from land-dwelling ancestors. The earliest arthropods, according to the fossil record, were trilobites and crustaceans. Later, species of arthropods became numerous in fresh water and eventually upon land, where the existing species of insects far outnumber the known species of all other living forms. Many of these insects now live in fresh water, but they have clearly descended from land dwellers that intervened between such fresh-water species and remote aquatic ancestors. The story in chordates has been told in Chapter 19. Simple marine animals and later fishlike ancestors are suggested by the facts of anatomy and embryology and by the fossil record. The invasion of the land by primitive forms transitional from fishes to the early Amphibia is clearly indicated, and from these explorers of the land surface the early reptiles emerged as the first chordates to be adapted for an existence upon land completely independent of an aquatic habitat. From reptiles came the birds and mammals with their further adaptations to terrestrial conditions. But throughout their history some of these land-adapted reptiles, birds, and mammals, such as the alligators and turtles, the many shore and water birds, and the seals and whales, have returned to the habitat of their aquatic ancestors and been modified accordingly. The evolution of animals coming out of the water has thus been matched to some extent by animals going back to the water in the subsequent course of their evolution.

HISTORIC FACT OF ORGANIC EVOLUTION

The evidence that has led biologists to conclude that the innumerable species of animals and plants now living and all the species that

lived in the past have arisen by an evolutionary process may now be presented. In so doing we shall be considering what has been called the fact of evolution and the course taken in particular instances. Although this evidence for organic evolution as the fact is subject to the limitations of all historic data, it has proved convincing because so many special cases tell the same kind of story. Perhaps no one of the principal lines of evidence is sufficient in itself, but taken together they are overwhelming.

Evidence from Distribution

What is called geologic distribution is a study of the distribution of fossils and is included in paleontology, or the science of fossils. It

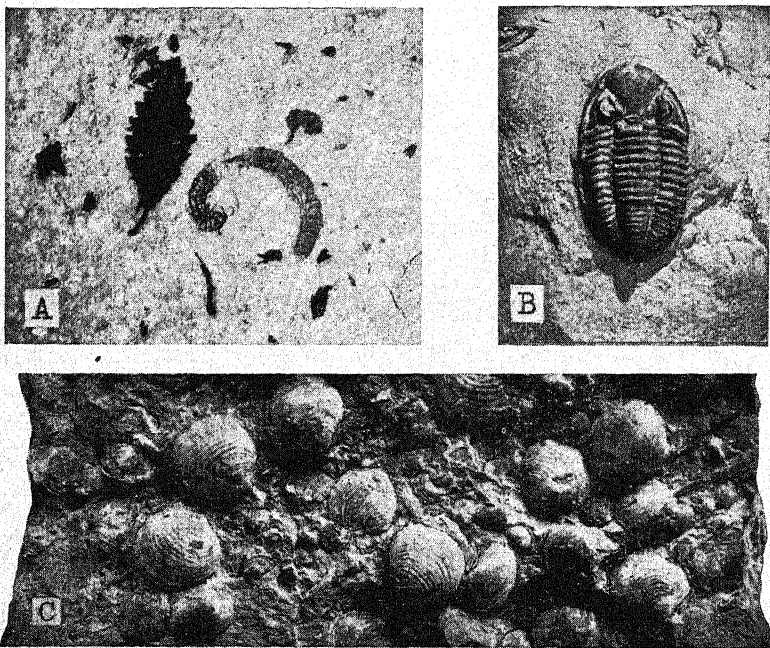


FIG. 471. Representative fossils. A, impressions of a leaf and of an insect larva. B, a trilobite, *Phillipsia griffithides*, representative of a great class of the Arthropoda that flourished in the Paleozoic Era (cf. Fig. 469), and later became extinct. C, a rich deposit of shells, principally the marine mollusk, *Astarte*. It was such remains as these (C) that led Leonardo da Vinci (1452-1519) to conclude that the rocks he observed in the high mountains of Italy had originated on the ocean's floor and hence that profound evolutionary changes had occurred in the history of the earth.

(Photographs by courtesy of American Museum of Natural History.)

may be contrasted with geographic distribution, which is the subject matter of zoögeography. These two kinds of distribution cannot be completely separated, since geologic distribution represents the geographic distribution that occurred in bygone times. In like manner the structure of fossil animals cannot be separated from that of existing

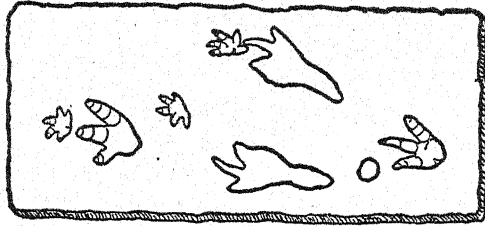


FIG. 472. Tracks of dinosaurs (*cf.* Fig. 473). *Above*, imprint left where a dinosaur sat down. *Below*, photograph of a slab of Connecticut Valley brownstone, from a specimen in the museum of Amherst College.

(From F. A. Lucas, "Animals of the past," 1916; courtesy of the American Museum of Natural History.)

forms if the animals now living are believed to have descended from those of the past. It is convenient, however, to discuss these two phases of distribution separately before explaining the correlations between them.

Geologic Succession. The remains or traces of animals and plants that occur in the rocks are known as *fossils*. Shells and other hard parts are buried in the sands and muds of river flats, lake beds, and ocean bottoms by the deposit of sediments. In time they may become petrified, or hardened into stony material, as water dissolves the

original substances and replaces them with others. Shells usually become filled with mud during burying, and later the shell itself may be dissolved by ground water after the mud has changed to rock. In this manner a mold of the shell may be formed. Shell-bearing animals usually leave only their shells, and vertebrates usually leave no remains except their bones and teeth. The soft parts of animals are never preserved in the rocks, although they may leave impressions as delicate as

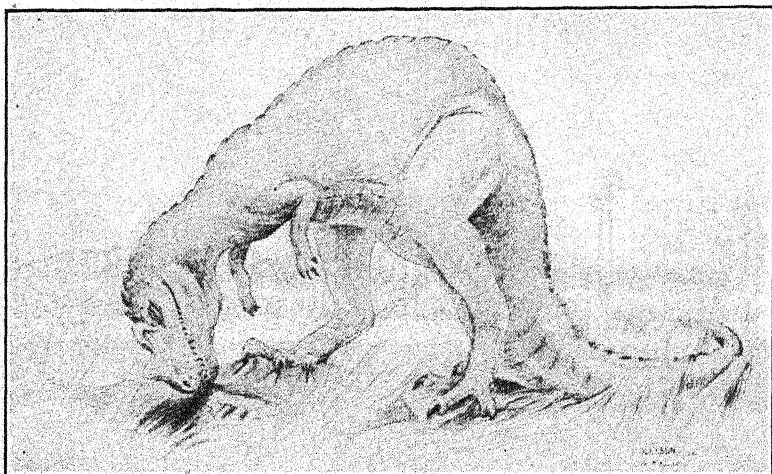


FIG. 473. Reconstruction of one of the carnivorous dinosaurs, *Carnotaurus*; shown feeding, with background of vegetation based upon associated fossils of plants. The dinosaurs were the dominant land animals in the Age of Reptiles (cf. Fig. 469), but became extinct as the mammals increased in numbers.

(From F. A. Lucas, *op. cit.*; courtesy of American Museum of Natural History.)

a human fingerprint. Even such an animal as a jellyfish might leave upon a beach of fine sand or mud an imprint that would be preserved if soon covered with fine sediment, as seems to have happened at least once. In a similar manner the tracks of small animals that have walked or crawled upon muddy beaches have become part of the fossil record, and the tracks of other animals, such as the great reptiles called dinosaurs, may be found in rocks where only occasional fragments of their bones remain (Fig. 472). Leaves buried in mud have formed the leaf-impressions that are often seen in collections of fossils (Fig. 471 A). Insects have sometimes been preserved in almost perfect condition after being caught in the resins of trees, as seen in the insect-containing amber of the Baltic region. Animals of the Glacial Period were sometimes frozen in the ice and snow and preserved, as was the mammoth found in Siberia (Fig. 475). The peat-bogs of the north and

the tar-pools of southern California contain the skeletons of animals that ventured upon the edges of the treacherous surface and sank to their death. But these are exceptions as compared with the great majority of fossils, which represent portions of the hard parts of animals and are embedded in sedimentary rocks (Fig. 471 C).

Although there is a wealth of such remains, the incompleteness of the fossil record must be recognized. Not only are the great majority of fossils merely fragments, but the known species cannot include more than the merest fraction of the animals and plants that have lived, because the chances are very small that the remains of any organism will ever become fossilized. Sometimes, however, skeletons are found that are almost complete (Figs. 476 and 477), and the record as a whole seems to give a fairly representative picture of the life existing in the past.

It is necessary to explain certain principles used by geologists in their study of the rock layers, if one is to understand the evidence for the *geologic succession* of animal types appearing in the fossil-bearing rocks. In view of the manner in which sediments are deposited in water, it is a truism to say that the oldest layers, or strata, are at the bottom and the youngest at the top when such deposits have been elevated above sea-level with no disturbance of their horizontal relationships. In many places this elevation has occurred without such disturbance as in Figure 479 A. In these cases it may be possible to recognize not only the fossils but also traces of the ancient topography, as when there are signs of beaches, mud flats, or deep water. In other parts of the earth, particularly in great mountain ranges, strata that were originally horizontal have been folded during their elevation (Fig. 479 D). The arrangement of the layers may be further complicated by the breaks known as "faults." By studying the rock outcrops in all parts of the world and the included fossils, geologists have pieced together a series of sedimentary formations resting upon the earlier igneous rocks and constituting the record of geologic

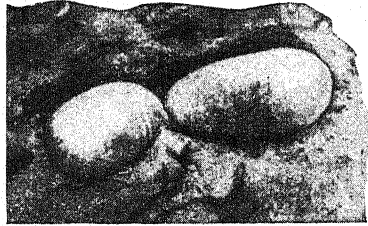


FIG. 474. Fossil eggs of a dinosaur, with the surrounding stone partially removed, as found in the Gobi Desert, Mongolia. These extinct reptiles presumably laid eggs like existing reptiles. The discovery of such eggs by the Third Asiatic Expedition of the American Museum of Natural History proves this for one species. In one instance the remains of a dinosaur embryo were found in an egg (cf. Fig. 453, p. 619).

(From Report, Field Museum of Natural History, vol. 7.)

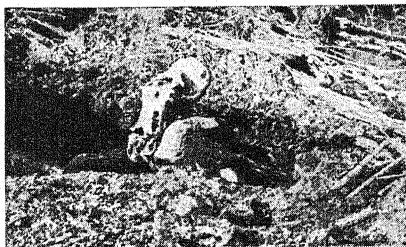


FIG. 475. Mammoth found frozen in a cliff in Siberia. *Above*, the specimen partially uncovered, showing skull and forefeet. *Below*, specimen as mounted in Zoölogical Museum at Leningrad. The animal had slipped into a crevice from which it was unable to extricate itself and had been covered with snow, which hardened into ice, before the flesh could decompose.

(Adapted from O. F. Herz, Annual Report Smithsonian Institution, 1903.)

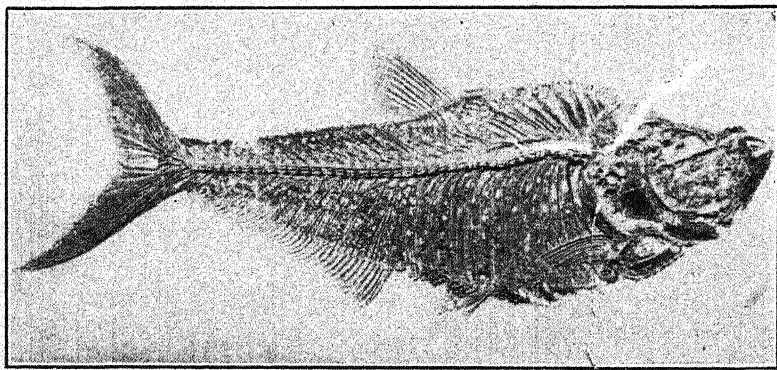


FIG. 476. An ancient member of the shad family, *Diplomystus*, from the fishbed at Green River, Wyoming.

(From F. A. Lucas, "Animals of the past," 1916; courtesy of American Museum of Natural History.)

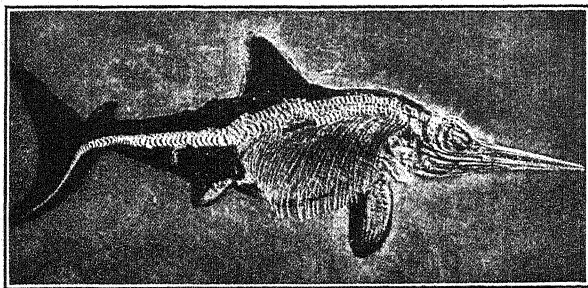


FIG. 477. An ancient reptile, *Ichthyosaurus*, adapted for aquatic life like the whales among mammals at the present time. This is an unusual fossil since the outline of the body is shown by a darkening of the rock due to carbon from the flesh.

(Courtesy of American Museum of Natural History.)

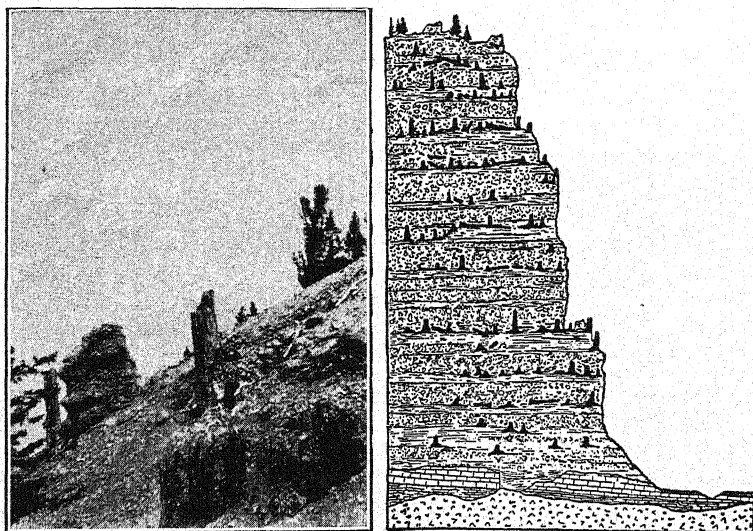


FIG. 478. Representative fossil records. *Left*, fossil tree trunks. *Right*, section of Amethyst Mountain, Yellowstone National Park, showing by fossil tree stumps that at least seventeen forests became established and were successively killed by deposits of volcanic ash. Some two thousand feet of rock are shown, and the whole rests upon other strata that show unconformity due to erosion of earlier land surfaces (cf. Fig. 479).

(*Left*, photograph by courtesy of American Museum of Natural History. *Right*, after W. H. Holmes, photograph by courtesy of H. F. Cleland.)

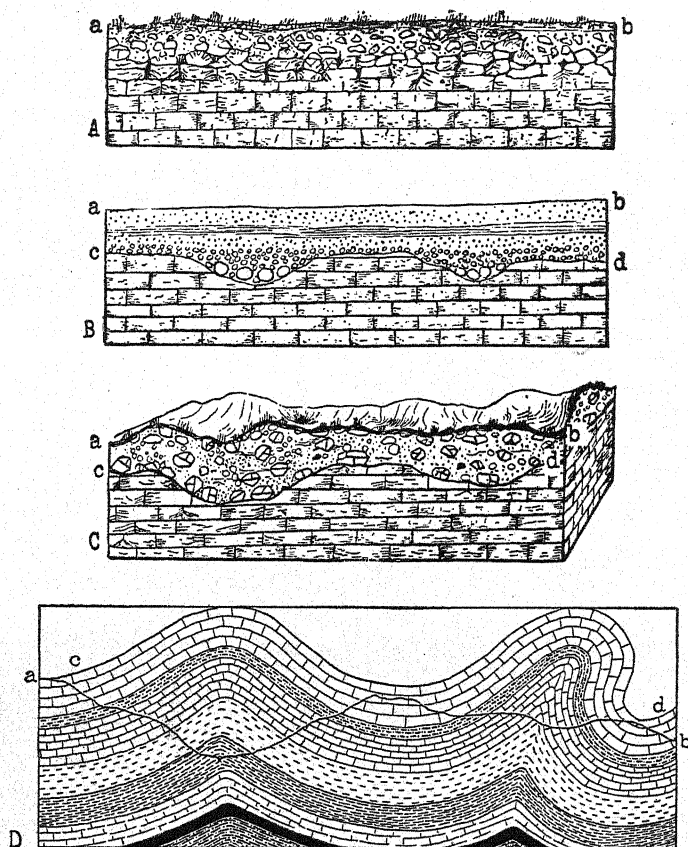


FIG. 479. Evidence of geologic evolution. A, section of an exposure in which the underlying solid rock has weathered into loose mantle rock and overlying soil (*a-b*). B, section showing a former land surface (*c-d*), upon which boulders, gravel, and sand have been deposited by flowing water, as indicated by the horizontal layers (*a-b*). C, section similar to B showing a former land surface (*c-d*), upon which are glacial deposits as indicated by the irregular distribution of boulders, gravel, and sand (*a-b*). D, section of a mountainous region, showing how the folding of the rock layers and the former land surface (*c-d*) can be reconstructed by study of the angles at which the rock outcrops occur on the existing land surface (*a-b*), which has resulted from the erosion (cf. Fig. 478).

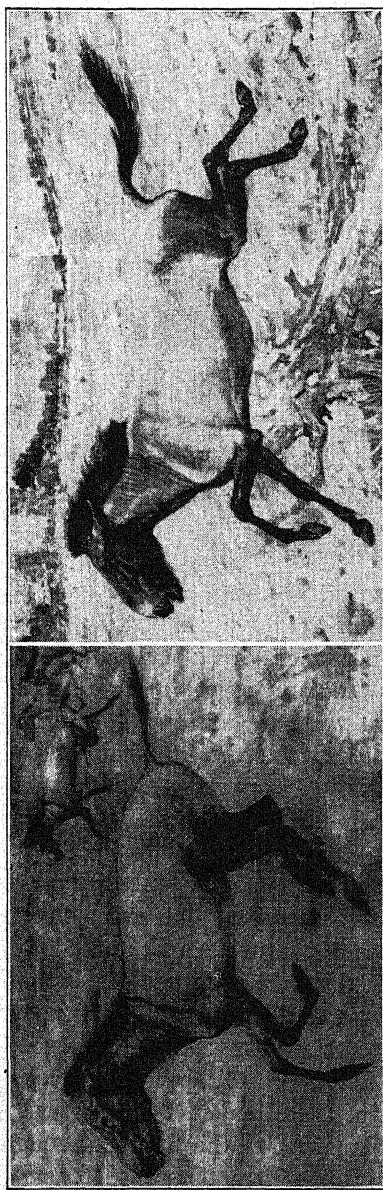
(A to C, after E. B. Branson, 1918, University of Missouri Bulletin, vol. 19.)

history (Fig. 469). The fossils in these strata indicate the order of appearance or succession of the various forms of life.

In the record as it thus appears, there is a succession from simpler to more specialized types, which is of the greatest significance for organic evolution. Not only are the animals of the past different from those of the present, but the record begins with forms that are vastly different. These are gradually succeeded by others that become more like existing species until they merge with those now living. There are many gaps, and many types have become extinct, but the geologic succession shows the grand course of evolution so far as it can be ascertained from the fossil record.

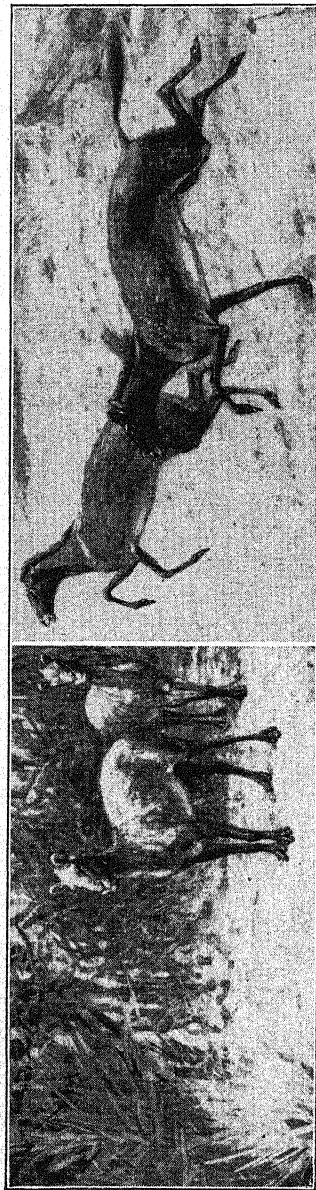
Special Examples of Geologic Succession: *Invertebrates*. There are many instances among invertebrate animals, particularly in mollusks and brachiopods, where the succession of fossils shows the course taken in evolution. A well-known example involving a large group is that of the extinct forms called *Ammonites*, which were cephalopod mollusks that flourished in Paleozoic times (*cf.* Fig. 323, p. 437). Beginning with the so-called nautiloid type in the Ordovician, the fossils show a succession that culminated in greatly specialized shells and such a wealth of species that the *Ammonites* were for a time the dominant forms of marine life. Later, the *Ammonites* became extinct, but the ancient nautiloid type persisted as the Genus *Nautilus*, which is still living in the Philippine region and in the Indian Ocean. Thus *Nautilus* has preserved its original organization, without substantial changes, throughout a span of geologic time sufficient for the evolution of the entire series of vertebrate animals. This is an exceptional case, however, since the vast majority of animals have been modified during the passing ages or become extinct.

The Horse Family. The fossil record of horses is probably more complete than that of any other mammalian type. The series shown (Figs. 480 and 481) occurs in fossil beds of the western United States, where horses flourished for a long period before they became extinct during the Pleistocene. In more recent times the members of the horse family, including horses, wild asses, and zebras, have been found only in Europe, Asia, and Africa. The wild horses of the Americas in recent centuries were the descendants of horses that escaped from the early explorers and settlers. In further explanation of the figure, it seems probable that the ancestors of the earliest American horses, such as the dawn-horse, *Eohippus*, originated in some other region and migrated to North America, since they appear suddenly in the fossil record without antecedent types. Central Asia is suspected as the place of origin, although the ancestors of *Eohippus* have not yet been discovered. After



Neohipparion, Miocene, South Dakota.

Equus scottii, Pleistocene, Texas.



Eohippus, Eocene, South Dakota.

Meshippus, Oligocene, South Dakota.

FIG. 480. Reconstructions of fossil horses (cf. Fig. 481 for relative sizes).

(Courtesy of American Museum of Natural History.)

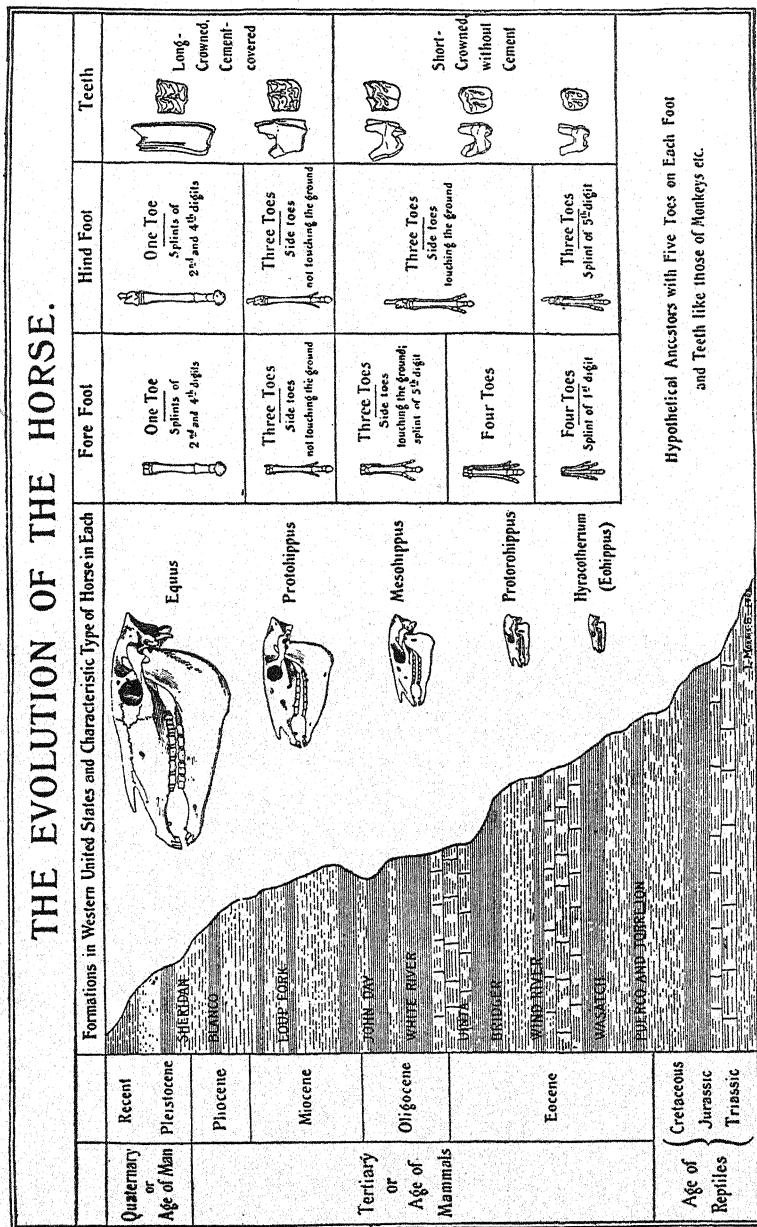


FIG. 481. Evolution of the horse family (cf. Fig. 469 for time-scale).

(From W. D. Matthew, courtesy of American Museum of Natural History.)

the horse family had flourished for a considerable period in North America, some of its members migrated to South America, if we may judge from the fossils, and spread widely on that continent. This southern branch of the family became extinct in the Pleistocene, as did the North American horses. The causes of this extinction, like the disappearance of Ammonites and many other types that have flourished

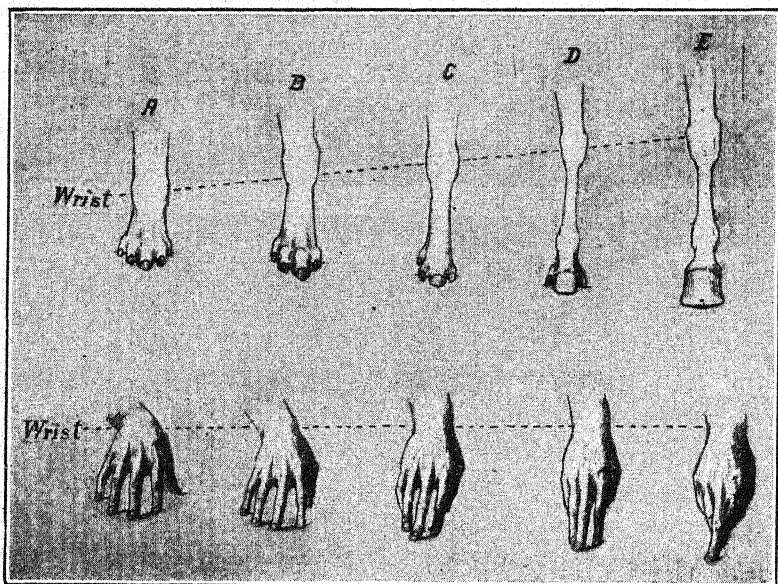


FIG. 482. Comparison of stages in evolution of the fore foot of horse with the human hand.

(Courtesy of American Museum of Natural History.)

and declined, remain a matter of speculation. One possibility is that all the horses of the New World may have been swept away by some disease-producing parasite. We only know that they disappeared in the Americas, while a few species survived on the continents of the Old World, perhaps after migrating to that region as the ancestors of the original American horse family seem to have migrated into the New World from an unknown locality.

The probable course of evolution by which forms like *Eohippus* became changed into horses of the modern Genus *Equus* is indicated by the fossils (Figs. 480 and 481). The series begins with an animal about the size of a fox, with relatively short neck and limbs. The feet are also short, and there are four functional toes on the front foot and three on the hind foot. The hind foot has splintlike remains

of two other digits, as though a man should have three toes functional and the little toe and great toe rudimentary. Since similar rudiments of a fifth toe occur on the fore feet, it appears that the ancestors of *Eohippus*, and therefore of modern horses, were five-toed (Fig. 482). The principal evolutionary changes, as shown by the succession of types, are the loss of side toes until only one functional digit persists; consolidation of leg bones so that the radius and ulna and the tibia and fibula become fused; increase in complexity of the teeth for the functions of grazing with the incisors and grinding with the molars; increase in size of the brain; and a great increase in size of the whole body with changes of shape and proportions, particularly in the head, neck, and back. In the modern horse there is only one fully developed digit, but there are splint bones on the fore limbs representing the rudiments of two others, and in the embryo there are additional digits upon fore and hind limbs.

The Elephant Family. The succession of types that are believed to be ancestral to the elephants of the present day is another example of a relatively complete fossil record (Fig. 483). The earliest known representative of the elephant family, *Mærittherium*, appears in the rocks of the late Eocene in the Libyan Desert of Africa. Types that are believed to have descended from this one may be traced to all the other continents except Australia. In the progenitor there is no proboscis, and the head has no obvious resemblance to that of a modern elephant. As we pass through the series, the snout becomes elongated to form the proboscis; the jaws become shortened in the line of descent that gave rise to the present-day elephants; the teeth become modified; and there is a great increase in the size of the body and of the brain. Like the horses, the elephants became extinct in Europe and North America at the close of the Pleistocene, although members of the elephant family had ranged widely upon these continents during epochs when the group was flourishing (*cf.* Fig. 475). The mastodons, which were the only type to reach South America, also became extinct in recent times. The only survivors are the African elephants and those native to southern Asia.

Synthetic Types. It is sometimes said by critics of evolution that the links which should exist between various animal types are not to be found. The foregoing discussion of fossil records shows that such links, or synthetic types, are not to be sought among existing animals but among fossils, since the links are the common ancestors. Thus, the connections between modern horses, zebras, and wild asses are the members of the horse family that were ancestral to these types. The links between the Asiatic and Indian elephants, and between the exist-

ing camels and guanacos, are likewise the extinct ancestors (Fig. 485). The links between men and apes are the extinct prehuman races (cf. Figs. 497-501).

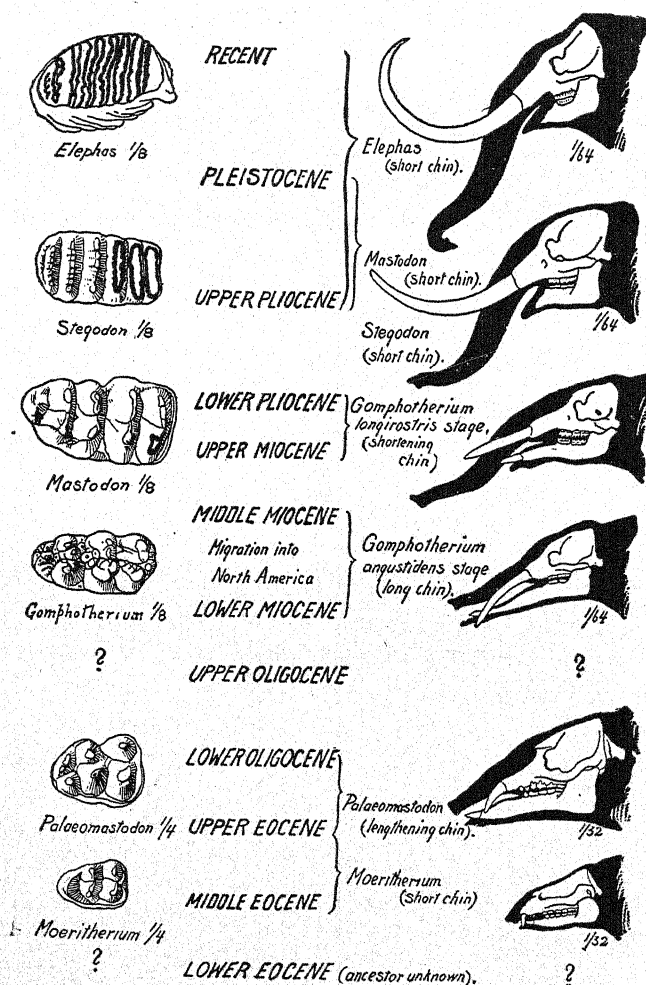


FIG. 483. Evolution of the elephant family (cf. Fig. 469 for time-scale). On the right, a series of skulls. On the left, the last lower molar tooth of the animal on the right.

(From W. B. Scott, "A history of land mammals in the western hemisphere," copyright, 1913, by The Macmillan Co., reprinted by permission.)

Connections between larger groups are not wanting, as in the fossils transitional between amphibians and reptiles, between reptiles and birds, and between reptiles and mammals, that are described in

Chapter 19, although in these instances no one animal shows all the transitional structures. Spectacular examples are the primitive birds that show reptilian features, notably *Archæopteryx* (Fig. 484). The development of birds resembles that of reptiles (cf. Figs. 72 and 73, pp. 126 and 127), and their adult structure resembles that of reptiles more than would be supposed from casual examination. As Huxley put it,



FIG. 484. *Archæopteryx*, an extinct and primitive bird. *Left*, one of the fossils as preserved in fine-grained stone. *Right*, a reconstruction of this fossil. The feathers and general shape of body are those of a bird, but the teeth, the tail, the claws on the wings, and other features are reptilian.

(*Left*, from F. A. Lucas, "Animals of the past," 1916; courtesy of American Museum of Natural History. *Right*, from T. J. Parker and W. A. Haswell, "Textbook of zoölogy," copyright, 1921, by Macmillan and Co., Ltd., reprinted by permission.)

birds are "glorified reptiles." *Archæopteryx* is perhaps as nearly a synthetic type as one could hope to find in view of the imperfections of the fossil record. In addition to such types within the fossil record, others that have been called "living fossils" are now in existence. The duckbill, which is an egg-laying mammal (Fig. 462, p. 632), may be regarded as a survivor not far removed from the egg-laying reptilian ancestors of mammals. The existing lungfishes (Fig. 443, p. 606), may be regarded as links between aquatic and terrestrial vertebrates that might have become extinct like *Archæopteryx* but have survived to

the delight of zoölogists. Even whole groups, such as the sharks or the amphibians, may be regarded as survivals of ancient types that have descended with modifications but without changing certain primitive features. Many of the large groups of animals show similar survivals. The continent of Australia has so many of these survivors among the Mammalia it has been called the "land of living fossils."

Geographic Distribution. In considering the subject of geographic distribution it is necessary to have in mind two fundamental conceptions. First, the ancestors of related genera, for example, originate in a single locality which is known as the *common center* of origin. Second, as the ancestral type becomes established and increases in numbers, *migration* occurs, presumably resulting from the search for food. The final direction of such migration seems to be determined by *barriers* that are in many cases geographic. For example, a large body of water blocks the migration of land animals, and high mountains or deserts are barriers to animals unable to withstand low temperatures or excessive dryness. Migration from a common center of origin in search of food and as directed by barriers is thus believed to account for the natural distribution of animals on land surfaces. The state of distribution effected by nature after countless years has been increasingly disturbed by human migrations and the consequent transportation of plants and animals to new habitats.

The study of geologic distribution includes both the lateral distribution of fossils, which indicates past distribution over the surface of the earth, and their vertical distribution, which indicates relative age. For example, study of the horse and elephant families includes the distribution of species over the various continents and their order of appearance in geologic epochs. Hence, the problems of paleontology are inseparable from those of zoögeography, or the geographical distribution of animals at the present day. The camel family illustrates this interrelationship. Approaching the problem from the standpoint of present geographical distribution, we find that this family consists of two widely separated types. The Genus *Camelus*, which includes the animals called camels, consists of two species: the one-humped Arabian camel, or dromedary, and the two-humped Bactrian camel of Central Asia. On almost the opposite side of the world, in the Andes of South America, are the only other camel-like animals now in existence: the Genus *Auchenia*, with its two species, the guanaco and the vicuña, and their domesticated descendants, the llama and the alpaca. The surprising separation of these two genera of a single family becomes intelligible when their geologic distribution is examined (Fig. 485). As the fossil record shows, camels originated as a family of hoofed mammals in

North America, where they flourished from the Eocene to the end of the Pliocene epoch. During the Pliocene they migrated, on the one hand, to South America and, on the other, to Asia by way of a former land connection in the Bering Sea region. The extinction of the North American forms during the Pleistocene left representatives in South

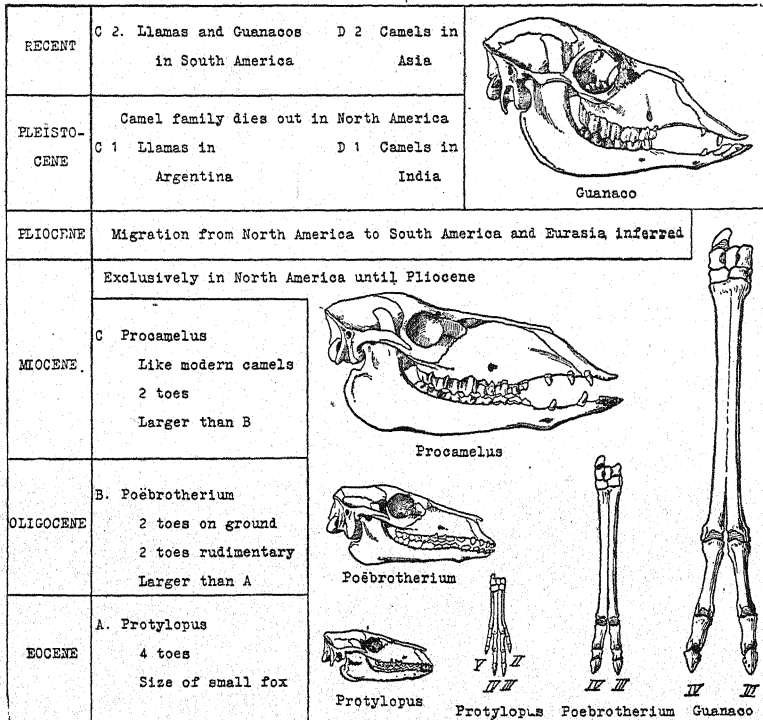


FIG. 485. Evolution of the camel family (cf. Fig. 469 for time-scale).

(Figures from W. B. Scott, "Theory of evolution," copyright, 1917, by The Macmillan Co., printed by permission.)

America and in Asia, from which existing species have descended. The seemingly inexplicable separation of the two branches of the family finds an explanation in terms of evolution and past migrations. Numerous other examples could be cited from the fossil records, all showing that the evolutionary theory gives meaning to the geographic distribution of many types of animals.

Frequently it is possible to explain the peculiarities of an entire fauna, or animal population of any particular locality, by the extension of a similar line of reasoning. Island life is an illustration. There are, geologically speaking, two types of marine islands: continental islands,

such as the British Isles and Long Island, and oceanic islands, such as the Azores, Bermuda, and the Hawaiian Islands. Continental islands are not far from continents, of which they seem to have been a part at one time; oceanic islands have appeared in the ocean without previous connection with any continent, or they are surviving elevations of continents that have existed in the past but have never been united with the well-known continental areas. The faunas that are found upon these two types of islands bear out the theories of their geologic origin and of the origin of faunas by evolutionary processes. Without going into details, it may be said that the native fauna of the British Isles is like that of northwestern Europe, because these islands were recently part of the neighboring continent. The native fauna of the Hawaiian Islands, on the other hand, is an odd mixture and unlike that of any continent, because these islands have had no recent connection with any continent and are presumably populated by animals and plants brought to them by chance, on floating objects or otherwise. Only from some such parentage could originate the bizarre combinations that commonly occur in the faunas of oceanic islands. Again, the continent of Australia has a fauna very different from that of Asia, because the two have been so long separated. Eurasia, Africa, and North America have similar mammalian faunas, because of former connections, or land bridges, across Bering Sea and by way of Greenland.

Evidence from Morphology

Comparative Anatomy of Adults. Whether one examines the broader features of anatomy in the several phyla of animals or the structure of a single class, such as vertebrates, he finds everywhere facts that are most reasonably interpreted by evolution. In the vertebrates two pairs of limbs, a body, head, tail, and various internal organs are always laid down according to a similar general plan but with special modifications in relation to the mode of life. It is, therefore, possible to construct a plan representing not any particular vertebrate but vertebrates in general (Fig. 437, p. 598). A similar plan can be made of other groups, as has been indicated in the accounts of the several phyla given in preceding chapters. Thus, the coelenterate body-plan, the annulate body-plan, the arthropod body-plan, and the vertebrate body-plan may be constructed. More specific resemblances are seen in the corresponding parts of the body when comparisons are made among the animals of a single class. The flipper of a whale, the wing of a bird or a bat, the fore limb of a horse, and the arm of a man all show the same general plan of structure despite their differences

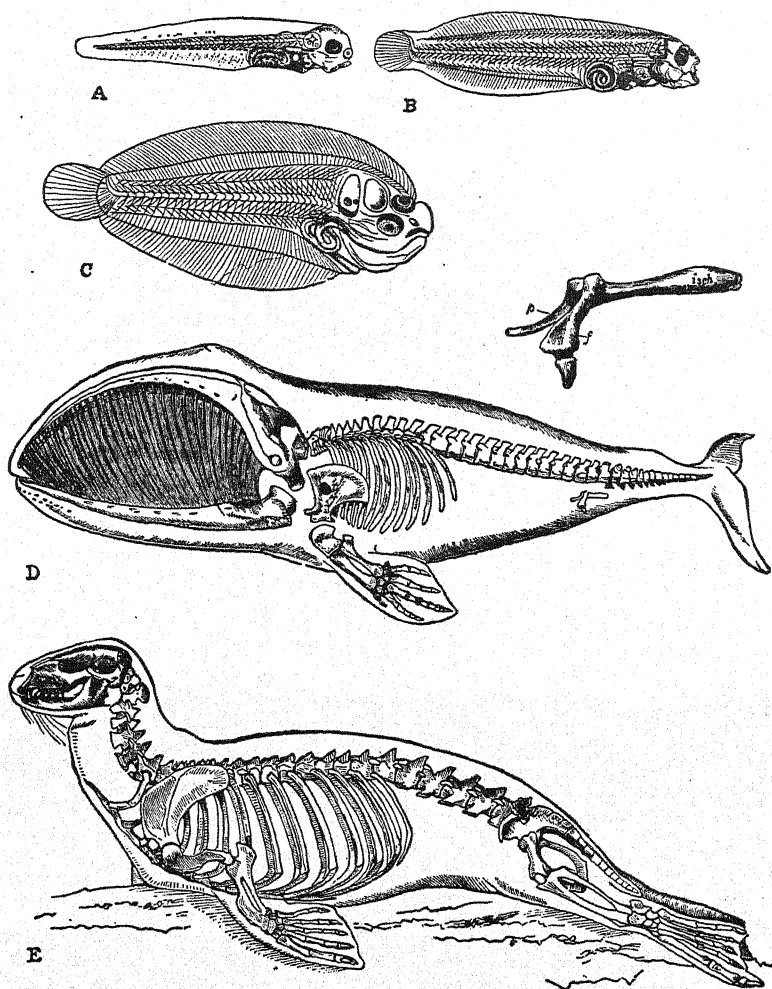


FIG. 486. Evidence for evolution from comparative anatomy and embryology. A to C, stages in development of the flounder, *Pleuronectes*, a fish that begins as a symmetrical type and changes during development to one with both eyes on the right side of the body. D, whalebone whale, showing bones in the flipper like those in the fore limbs of typical terrestrial mammals (cf. Fig. 36, p. 67, and Fig. 38, p. 69) and vestiges of pelvis and hind limbs; the pelvis with its pubis (*p*) and ischium (*isch*), and the femur (*f*) are shown on larger scale. Plates of whalebone are attached to upper jaw. Both jaws are toothless in adult, but there are vestigial teeth in embryo. E, seal, another type of mammal adapted for aquatic life.

(A to C, after L. Agassiz, from H. E. Ziegler, "Lehrbuch der vergleichenden Entwicklungsgeschichte," 1902; D and E from G. J. Romanes, "Darwin and after Darwin," copyright, 1896, by Open Court Publishing Co., reprinted by permission.)

(Figs. 486-488). Comparable resemblances between parts could be cited from every group of animals. This fact of resemblance in plan, whether of the body as a whole or of its special parts, is the great principle of *homology* (cf. p. 237), which is illustrated in every phylum of the Animal Kingdom.

What are called *vestigial structures* are important in this connection. These are structures which correspond in plan and position to functional parts of related animals but are reduced in structure and may be

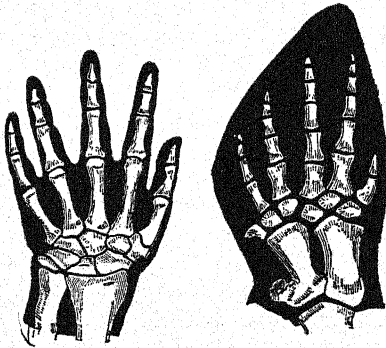


FIG. 487. Hand of man and flipper of whale (cf. Fig. 36, p. 67, and Fig. 38, p. 69).

(From J. G. Romanes, *op. cit.*, reprinted by permission.)

without obvious functions. For example, in the modern horse there are two splint bones, which are vestiges of the second and fourth digits. In the python there are vestiges of the hind limbs that are entirely absent in most snakes, and certain aquatic mammals have only vestigial hind limbs (Fig. 486 D). On the other hand, some of the running birds have vestigial fore limbs. Such vestigial structures are numerous especially among the more specialized members of any phylum.

For the purposes of this discussion, the question is: What do these facts of anatomy indicate regarding

the history of animal life? The pre-evolutionary explanation was that each species of animal, although created separately, was nevertheless formed in accordance with an ideal type, hence the homologies. This was the belief of Louis Agassiz (1807-1873), who was unable to adjust his thinking to the concept of evolution as set forth by Darwin in 1859. Such an idea is a theoretical possibility, provided there is evidence that animals originated by creation in their present form and have not changed. However, animals do not seem to have originated in their present form, and they do seem to have changed during geologic time. The evolutionary explanation of these anatomical resemblances between animals is that the members of a group, such as the vertebrates, have inherited a similar plan of organization from the ancestors that all vertebrates had in common. Each subdivision and species has been modified in particular ways in relation to its habits of life. But they remain fundamentally alike, because they have never lost the underlying plan of body that existed in their ancestors. Because whales and horses and all other mam-

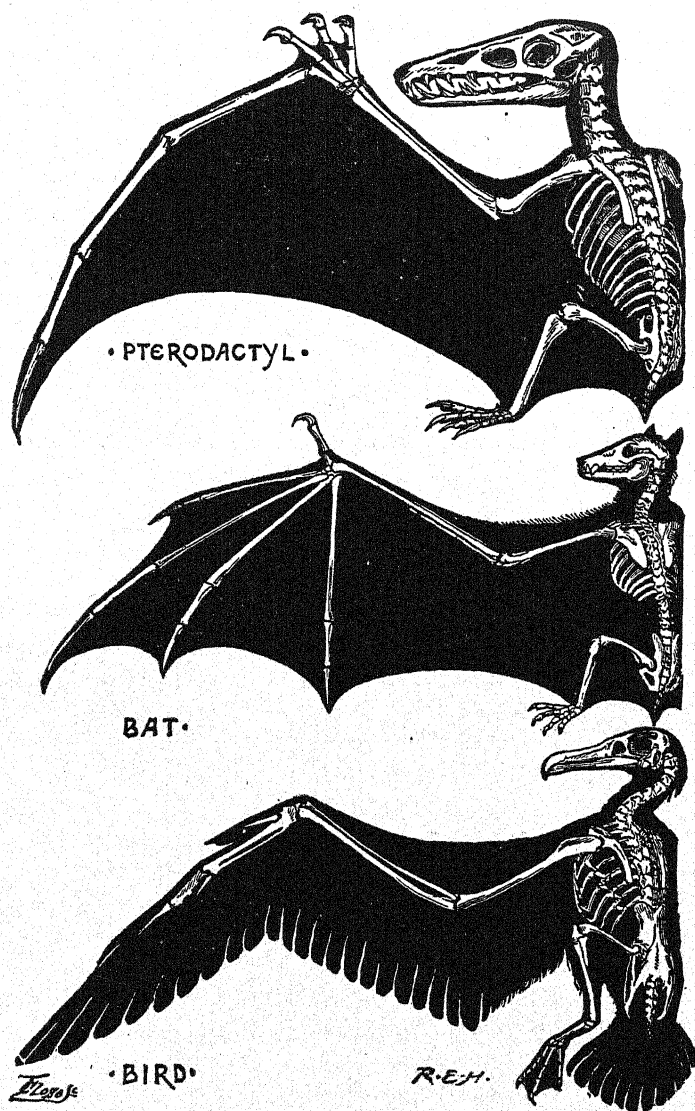


FIG. 488. The wing of a pterodactyl, an extinct flying reptile; of a mammal, the bat; and of a bird; showing three modifications of the anterior appendage (cf. Fig. 36, p. 67 and Fig. 38, p. 69).

(From G. J. Romanes, *op. cit.*, reprinted by permission.)

mals had a common ancestry at a remote period, their fore limbs and many other parts have certain similarities today. Mammals resemble other vertebrates for a similar reason. Vestigial structures remain because they are part of a persistent plan and have not been entirely lost, although they may be no longer functional. The comparative anatomy of adult organisms is what might be expected if evolution has occurred.

Comparative Embryology. Almost everyone who knows anything of the evidence for organic evolution has heard the statement that the development of an individual is a repetition of the development of the race. This *Recapitulation Theory*, as it has been called, maintains that certain developmental stages or structures are related to ancestral conditions, although it recognizes that others may be adaptations to the present manner of development.

To cite a familiar example, the embryo of a fish develops gill slits, gills with blood vessels, and a two-chambered heart, all of which persist in the adult. The tadpole of a frog develops a similar organization which is fishlike in the arrangement of gills and blood vessels and in the two-chambered condition of the heart. But these structures are completely reorganized during the development, which culminates in a metamorphosis by which the tadpole changes into an air-breathing animal with lungs and a three-chambered heart (Fig. 450, p. 615). In reptiles, birds, and mammals, the embryo develops rudimentary gill slits and a fishlike circulatory system, only to have these parts reconstructed in later stages to form a different adult organization (*cf.* Fig. 89, p. 148, and Fig. 496). These stages of development in vertebrate embryos are as well known as any facts in the anatomy of the adult animal and can be seen by any student of embryology. Such stages might be expected in fishes and perhaps in the amphibians, which develop in water; but not in reptiles, birds, and mammals. When, however, this course of development is viewed in the light of an evolutionary interpretation, it is what might be expected. If the ancestors of vertebrates were originally fishlike animals (*cf.* Fig. 438 and 445, pp. 599 and 609), it is seen that the amphibians represent a transition from aquatic to terrestrial life and that their development has been modified accordingly. The reptiles, birds, and mammals are true terrestrial animals in their mode of development and in their adult condition. The later stages have been modified, but the early stages still resemble those of fishes. It is not correct to say that the embryo of a reptile, a bird, or a mammal is a fish at any stage of its development, but it can be said that such embryos resemble the embryos of fishes at corresponding stages. The statement that the animal "climbs the ancestral tree" in the course of its development is likewise unfortunate. It can

be said that many animals have in the course of their development structures that disappear or become greatly modified in the adult individual. And in many such cases there is reason to think that structures now transitory were formerly present and functional in the adult as well as in the developmental stages. Thus, the fish embryo becomes an adult that is not unlike the embryo, while the embryo of a terrestrial vertebrate develops the adult organization of the reptile, bird, or mammal. The individual development, or *ontogeny*, is not a repetition of ancestral development, or *phylogeny*, but certain structures that are reminiscent of ancestry may be found in embryos. As with adult anatomy, such facts of development are only to be expected if evolution has occurred.

Classification. Animals and plants may be classified in a variety of ways. They can be grouped according to their habitat, by separating fresh-water animals from land animals, the animals of forests from those of prairies, and so on. Again, they can be classified according to their food, or even according to their size, as one classifies books by putting them in a bookcase to fit the shelf room. But just as there is one basis of classification that is the most natural for books, namely subject matter, so for living beings there is a natural classification, the basis of which is structure. When one classifies animals on this basis, he does no more than recognize and apply the principles of comparative anatomy and embryology. Such a classification expresses the degree of structural resemblance, as when a certain number of animals are placed together in the Phylum Chordata, the Class Amphibia, the Order Anura, the Family Ranidae, and the Genus *Rana*. A complete classification of the Animal Kingdom would be a family tree of animal life after the manner explained in Chapter 7. Indeed, classification merely summarizes evidence for evolution that is derived from morphology.

Evidence from Physiology

Similarity of the capacities of metabolism, irritability, and reproduction is additional evidence for evolution. Since all forms of animal life agree in these fundamental processes, one may reasonably suppose that all have descended from an ancestral protoplasm which possessed these capacities. Taken alone, this general uniformity of functions is much less impressive than the many special cases presented in the examples of structure and distribution, although it corroborates the evidence from other fields.

There is, however, one line of physiological evidence that is very impressive. It has been ascertained, by methods which need not be described here, that the blood serum of various animals shows certain chemical resemblances. Extensive tests have been made, particularly among vertebrates. Animals that are closely related, according to the classification based on structure, exhibit a parallel degree of relationship in the chemical nature of their blood. The blood of man, for example, is very much like that of a gorilla or a chimpanzee, less like that of a monkey, and so on, showing degrees of relationship that agree closely with the classification of the Mammalia. The blood of any mammal is more like that of other mammals than it is like the blood of birds or reptiles. Bird blood is like bird blood, reptile like reptile; but there is a closer resemblance between the blood of birds and that of reptiles than between that of either and the blood of mammals. This fact is to be correlated with the relationships between birds and reptiles inferred on other grounds (*cf.* p. 625). The numerous tests that have been made confirm the degrees of resemblance previously inferred from anatomy, embryology, and paleontology and expressed in classification. Among invertebrates, similar tests of tissue extracts show a greater chemical resemblance between chordates and echinoderms than between chordates and other invertebrates, a relationship that has been inferred on other grounds (*cf.* p. 557 and Fig. 135, p. 215). In like manner the mollusks show a chemical relationship with the annelids, as has been otherwise inferred (*cf.* Fig. 135, p. 215). Thus, evidence from physiology corroborates the much greater volume of circumstantial evidence from other fields. Related to such physiological resemblances between animals believed to have various degrees of kinship is the fact that related animals are frequently found to be susceptible to the same kinds of diseases. For example, man and the apes most closely related to him have certain diseases in common.

Evidence from Experimentation

Domestication of Animals. Evidence based upon experimentation is found in the history of animals and plants under domestication and in the experiments conducted by breeders and scientists. Domestic animals must have originated from wild ancestors that were gradually tamed by man, although in most instances there is no historic record of the original domestication. Some forms are still in the preliminary stages. The Indian elephant is not reared in captivity but is caught when nearly full-grown and trained. The attempts to domesticate the few surviving bison of the North American continent and the rearing

of certain fur-bearing animals in captivity illustrate possible beginnings of domestication in the present. In the great majority of cases, however, the original domestication occurred before the period of the earliest historic records.

In some animals, such as the domestic fowl and swine, the original wild species, from which all the domestic breeds seem to have de-

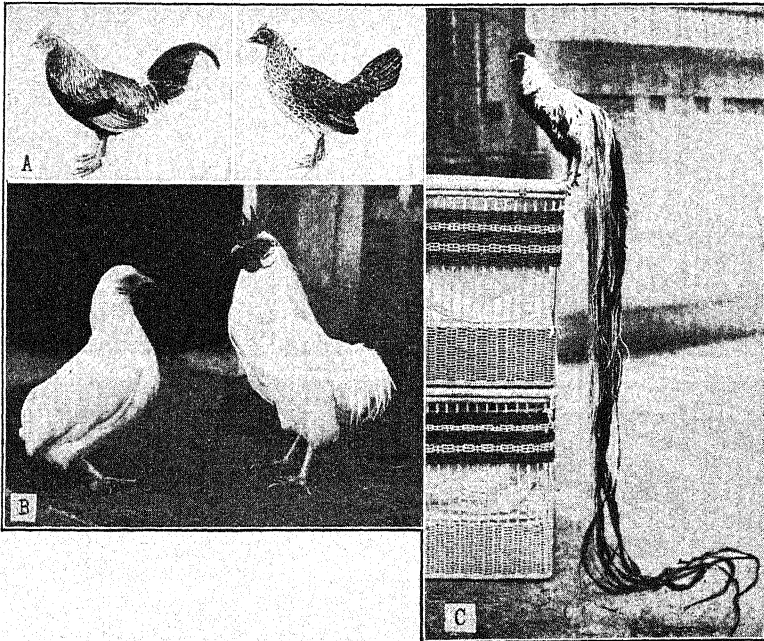


FIG. 489. A, the jungle-fowl, *Gallus bankiva*. B, tailless fowl of Japan. C, long-tailed fowl of Japan. All domestic poultry has apparently descended from the wild jungle-fowl of Southern Asia, intermingled to some extent with the wild Malayan fowl, or aseel.

(A, from C. B. Davenport, 1910, Carnegie Institution of Washington, Pub. 121.)

scended, can be determined with reasonable certainty (Figs. 489 and 490). In other cases, such as the dog, no single wild species can be so identified. The argument regarding evolution in all these cases is that many types, so different that they would be called species if found in nature, have actually originated from a limited ancestry under the eyes of man, although man was largely unaware of what was happening. Thus, there has been an origin of species among domesticated animals. From this fact one may argue, as Darwin did in his famous volume, that if one species can come from another, the process can

continue indefinitely, and, given time, any possible amount of evolutionary change can be produced. Certainly one could hardly expect greater changes in a few thousand years than seem to have occurred in the evolution of the many breeds of domestic poultry from the jungle-fowl and the Malayan fowl or the many breeds of pigeons from



FIG. 490. Evolution of domestic swine. *Above*, a wild hog, *Sus scrofa*, and its young. *Below*, a prizewinning Duroc Jersey barrow. The domestic hog of Europe and America apparently has descended from the wild hog of Europe, *Sus scrofa*, with some admixture from the wild hog of Asia, *Sus vitatus*.

(*Above*, from W. H. Flower and R. Lydekker, "Mammals living and extinct," copyright, 1891, by A. and C. Black, reprinted by permission; *below*, by courtesy College of Agriculture, University of Missouri.)

the wild rock-pigeon which was one of their most important if not their sole ancestor. The history of other domestic animals tells the same story (Figs. 491 and 492).

In one respect, however, these domestic species differ from wild species; they can usually be bred among themselves. Wild species seldom can be crossed. This is not such a serious objection as it might

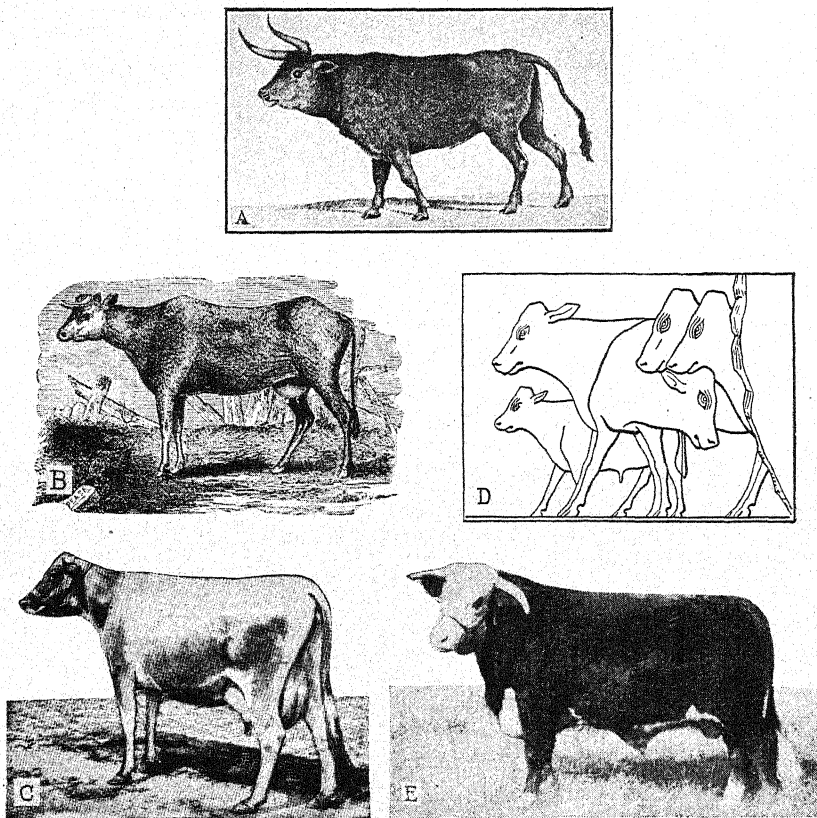


FIG. 491. Evolution in European and American cattle. *A*, an early figure representing the principal ancestral species, the urus or German aurochs, abundant in Europe and Britain during Roman times, but now extinct unless some of the herds preserved in English parks are survivors. *B*, an early type of the Jersey breed. *C*, modern Jersey. *D*, hornless breed of Egyptian cattle, not ancestral to modern hornless breeds, but showing that there were special breeds and hence a long antecedent domestication of cattle even in ancient times. *E*, modern prize Hereford steer, showing contrast with type *C*, which is bred for milk production.

(*A*, after G. Cuvier, "Animal kingdom," London, 1827; *B*, from the "Country gentleman," 1853; *C* and *E*, photographs by courtesy College of Agriculture, University of Missouri; *D*, after J. H. Breasted, 1919, Scientific Monthly, vol. 9, from a tomb relief at Gizeh, 29th century, B.C.)

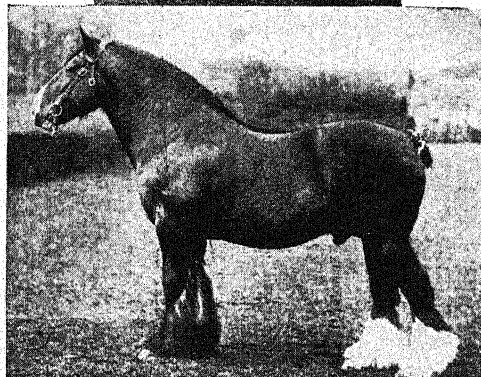
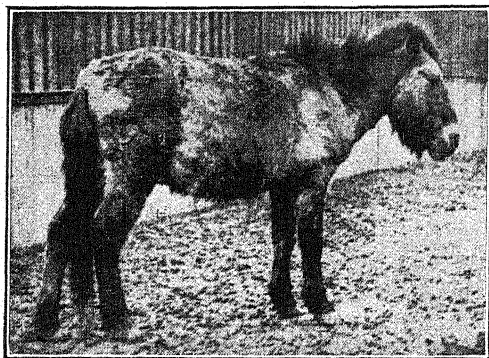


FIG. 492. Evolution of horses. *Above*, the tarpan, or wild horse of Mongolia. *Middle*, Shetland pony. *Below*, draft horse. It appears that the domestic horse has come from at least two original wild stocks. One species, represented by the Sewalik horse, was tall and slender-limbed, with broad forehead and tapering face. The other, represented by the tarpan, was a shorter and stouter-limbed type. The Shetland pony and draft horse have arisen from the generalized domestic type existing in northwestern Europe in Roman times.

(Tarpan from J. A. Thomson, "The outline of science," copyright, 1922, by George Newnes and Son, Ltd., reprinted by permission. Others by courtesy of American Museum of Natural History.)

seem, in view of the physiological adjustments that must exist in domestic as compared with wild animals. It is also true that domestic animals are modified to suit the needs or fancies of man and not their own needs, as are species in nature. They have been bred for this purpose, as natural species are bred in nature to meet the necessities of their lives or perish. Instead of a defect in the evidence, this situation might be regarded as an element of strength, since it shows that under one set of conditions certain characteristics can be evolved, whereas under other conditions different characteristics become established.

Production of New Breeds. The evolution that has occurred in domesticated forms, as described in the preceding paragraphs, has been brought about by the attempts of men to secure desired types of animals and plants. The early men who caught jungle-fowls and penned them up probably used the wilder ones as food or let them escape, and thus the tamer individuals survived to breed. In later times there was more conscious effort to improve the stock by crossing and by selecting only the desired types for breeding. Darwin tells us how in Saxony during the early nineteenth century men followed the breeding of sheep as a trade. "The sheep," he says, "are placed on a table and are studied like a picture by a connoisseur; this is done three times at intervals of months, and the sheep are each time marked and classed, so that the very best may ultimately be selected for breeding." Breeders continue to effect great changes and establish new breeds. A conspicuous example among plant breeders was Luther Burbank, who worked by crossing different types of plants in large numbers and selecting, out of many thousands, the ones that seemed most desirable, without adequate knowledge of the genetic factors involved. All such work tends to become increasingly scientific. Knowledge of the mechanism of heredity enables the scientific experimenter to excel any practical man who is ignorant of these principles. Illustrations of what can be accomplished by the application of scientific principles to the problems of breeding are seen in the production of desired varieties of wheat and corn and of various domestic animals. Attempts to produce new breeds thus merge with the effort to determine how evolution occurs under the conditions of scientific experimentation that are described in Chapter 6 on genetics.

Summary of Evidence

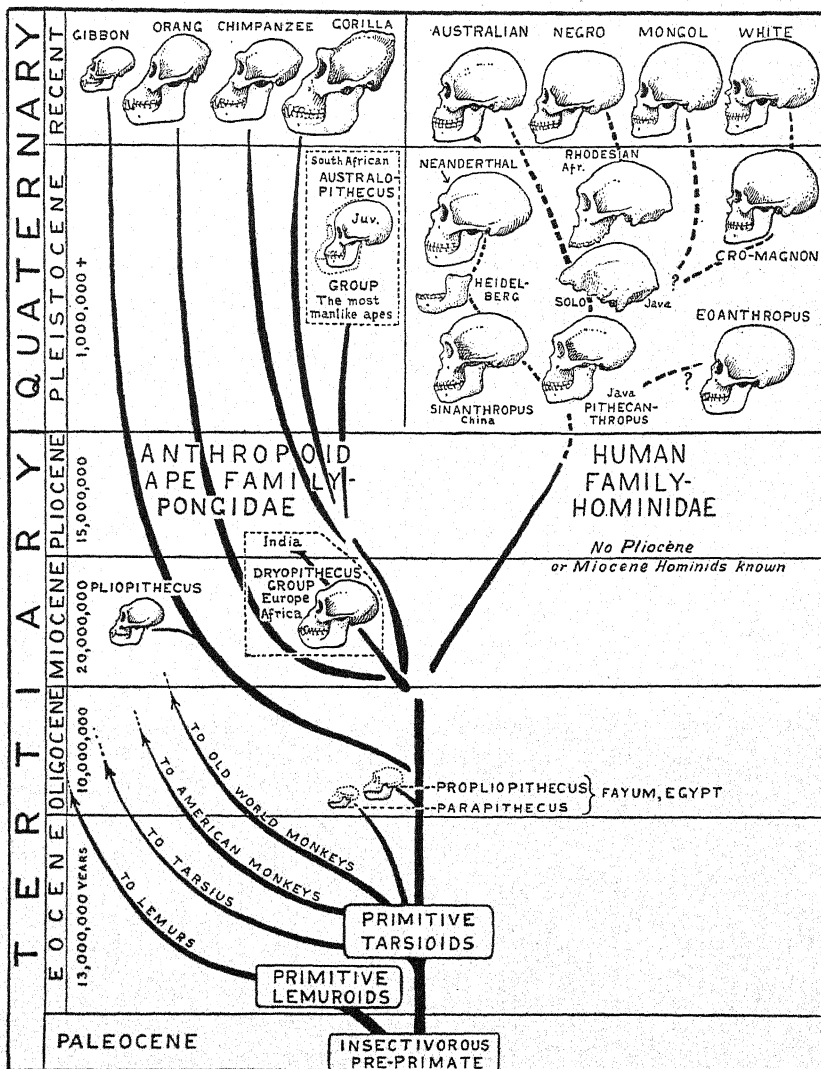
In summary of this evidence for organic evolution it may be said again that, because of evidence from many fields, biologists accept evolution as the historic course of events in the origin of new kinds of

animals. The fossil record of animals and their present geographical distribution can be most reasonably interpreted according to the evolutionary theory. Animals resemble each other structurally in varying degrees that seem to indicate the degrees of evolutionary relationship. The structure of animals and their mode of development are as we might expect them to be if evolution has occurred. Thus far, the evidence is indirect or circumstantial, but it is so extensive as to be convincing. In addition, there is the direct evidence that evolution has occurred among domesticated animals and is still occurring under the direction of skilled breeders and scientific investigators, although the factors involved have not yet been fully ascertained. The limitation of indirect evidence is that one does not observe the occurrence; but such evidence may be convincing if it is extensive and diversified. The limitation of the direct evidence for evolution is that so little change can be expected during so brief a period of observation. However, the evidence as a whole is convincing to the biologist.

Human Evolution

Man as a Primate. With the evolution of all other living beings thus attested, it is impossible to exclude man from the universal process of organic evolution. Human structure and development; the classification of mankind in the Family *Hominidæ*, closely allied to the Family *Pongidæ* (*Simiidæ*), or tailless apes; the fossil record; and the existing races of men all point to evolution as the one reasonable explanation of the facts. Paleontology shows that the Order *Primates*, which includes man, the apes, and the monkeys, arose from the general mammalian stock (Fig. 493). In more recent geologic times fossil remains of pre-human races indicate the line of man's descent. On the intellectual side, psychology is showing the animal nature of human intelligence, and the beginnings of morality are believed to be recognizable in the higher Mammalia. It is safe to assert that by another fifty years many other facts indicative of human origins will have been discovered.

The structure of the human body is fundamentally like that of other Mammalia, particularly the Family *Pongidæ*, which includes the four types of tailless apes: the gibbon, orang, gorilla, and chimpanzee. There is no essential detail of human anatomy that is not present in these apes, although the more erect posture of man has resulted in characteristic specializations of the pelvis and viscera, the fore limbs, the foot, and other parts. The brain, of course, is the most distinctive feature of man (Fig. 494). It is relatively larger than that of any other animal except very small vertebrates such as the humming bird.



J.H. MCGREGOR-MODIFIED FROM W.K. GREGORY ET AL.

FIG. 493. Ancestral tree of the anthropoid apes and mankind, showing also the bases of the branches leading to related forms (cf. Fig. 469 for time-scale). Certain parts of the tree are necessarily tentative, for example, the separation of anthropoid and human families. In *Parapithecus*, *Propliopithecus*, and the Heidelberg Race, only the lower jaws have been found; in *Pithecanthropus*, the skull cap and the other fragments have recently been supplemented by several skulls that are more complete; in *Australopithecus*, parts of two adult skulls of closely related forms have recently been found, supplementing the original find, which was the skull of a juvenile individual (cf. Fig. 498).

(From a drawing by J. H. McGregor, based upon data modified from W. K. Gregory et al., courtesy of J. H. McGregor.)

Another exception is that of certain very small American monkeys in

which the brain is relatively much larger than in man. Taken as a whole the specialization of brain functions exceeds that of any other mammal, but here again the structural and functional relationships are all paralleled in the higher apes. The psychology of these apes likewise resembles that of man. The evidence justifies the belief that the ancestors of man advanced to articulate speech and the development of hand and brain, whereas another line of descent, which produced the tailless apes, failed to progress in these respects as did the human ancestry.

Many features of the human body that are seemingly vestigial may be cited as evidence of man's kinship with lower animals. For example, the direction of growth of the hair on the arms and hands resembles that in the tailless apes, in which it seems related to the shedding of water when the arms are clasped above the head with the elbows pointing downward. Many such cases were cited in the post-Darwinian period (1859-1900). These and others have been given more critical examination during the past fifty years. It can be said in general that the differences between the Hominidæ and the Pongidæ are what might be expected in "cousins" removed by some millions of years (*cf.* Fig. 493) from their common ancestry.

What may be called embryonic vestiges are even more numerous. Vestigial gill bars and a fishlike blood system are formed in human

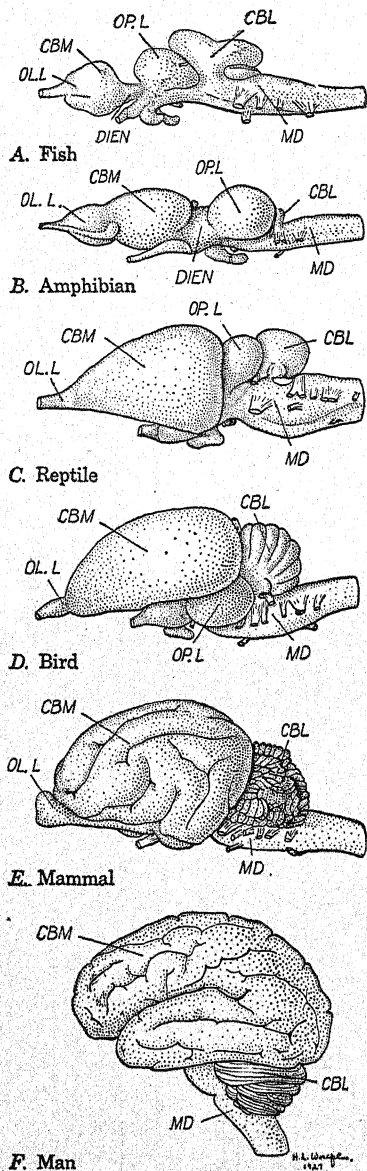


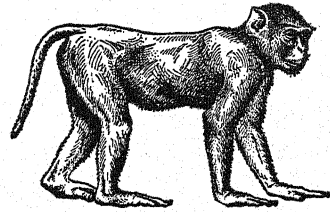
FIG. 494. Evolution of the vertebrate brain, as suggested by comparative anatomy of its adult structure (*cf.* Fig. 31, p. 61).

embryos as in those of other mammals (Fig. 496). A tail is noticeably developed in the embryo but becomes vestigial in the adult. At one stage of the embryonic life the entire body is covered with a well-developed coating of hair. The great anatomist Wiedersheim claimed that there are at least one hundred and eighty of these vestigial structures in the human embryo. These structural resemblances of adults and embryos are summarized by the classification of man in the Family Hominidæ, which is placed next to the Family Pongidæ, or tailless apes, in the Order Primates (Fig. 493).

Functional resemblances are implied in connection with the structures mentioned in the foregoing descriptions. For example, the running on all fours, which not infrequently is well developed by certain children (Fig. 495), is suggestive of the recurrence of an ancestral gait. General physiological resemblances are illustrated by blood tests, which show a close similarity between man and the higher apes, and specifically by the reactions to certain diseases and to parasites. For example, most, if not all, human diseases due to microorganisms can be transmitted to chimpanzees. Apparently, there is no essential physiological reaction in man that is not paralleled in the higher apes and even in the monkeys. These functional resemblances would not be so important in themselves, but they are very significant as corroboration of all the other evidence.

Evidence from Fossils and Artifacts.

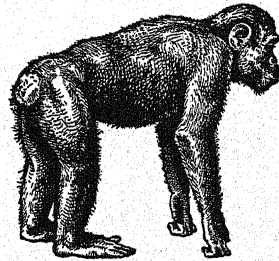
Further evidence of man's evolution appears in the remains of human and sub-human beings discovered in Africa, Java, China, Europe, and Palestine (Figs. 493 and 497-501). In most instances only



MACAQUE



HUMAN INFANT



CHIMPANZEE

FIG. 495. The four-footed gait, often seen in human infants, compared with that of a monkey (macaque) and an ape. Since the ape uses its hands in the more specialized manner shown, this gait in man must hark back to an anthropoid state earlier than that represented by the ape, if it is an ancestral reminiscence.

(After Hrdlicka from A. H. Schultz, 1936, *Quarterly Review of Biology*, vol. 11, reprinted by permission.)

fragments of skulls and the larger bones are found, but for certain races virtually complete skulls and complete skeletons have been discovered. Although the collections are increasing year by year, these records of human beings can never be comparable with those of animals more likely to be preserved as fossils. Fortunately, the human fossils are supplemented by artifacts, such as weapons and implements of stone or other enduring material (Figs. 502 and 503), by carvings (Fig. 504), and by signs of human activities, such as

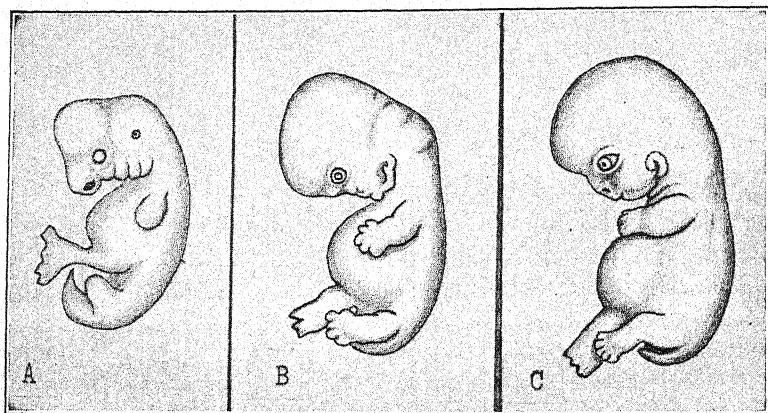


FIG. 496. Human embryo at three stages of development, showing rudimentary gill slits, tail, and limbs.

(Adapted from F. Keibel and C. Elze, "Normentafeln," 1908, and drawn by Wiley Crawford.)

fires and dwelling places. Often camp sites have been discovered, as indicated by the marks of fire, artifacts, bones of animals, and other débris, and yet there may not be a single skeletal fragment of the men who must have frequented those localities during innumerable years.

Although the most extensive series of human skeletal remains and artifacts have been found in the European region, man seems to have originated in Asia or perhaps in Africa. Close to the human ancestry are the great apes, such as the *Dryopithecus Group* (Fig. 493), found in Asia, Africa and Europe, and the *Australopithecus Group* (Fig. 498) in Africa. The latter, according to Figure 493, is classified with the apes, although its members are regarded as more like the Hominidæ than any other apes now known. The man of Java, *Pithecanthropus erectus* (Figs. 493 and 497 C), now seems even nearer the line of descent to modern man than had been previously supposed. A later find in Java, called *Homo soloensis*, is perhaps a descendant of *Pithe-*

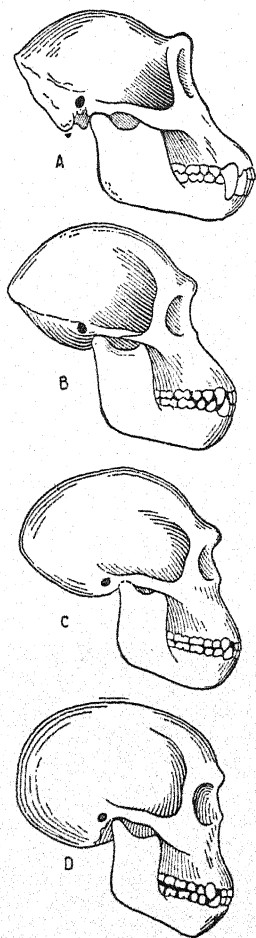


FIG. 497. Reconstructed skulls of anthropoid apes and pre-human races. A, adult chimpanzee. B, *Australopithecus africanus* (cf. Figs. 493 and 498). C, *Pithecanthropus erectus*. D, *Eoanthropus dawsoni*.

(From R. Broom, 1925, *Natural History*, vol. 25; courtesy of American Museum of Natural History and the author.)

canthropus. Other and more recent finds in Java are important, but their exact relationships are still disputed. The Peking man, *Sinanthropus pekinensis* (Fig. 499), discovered in the hills to the west of the ancient capital of China, was a primitive human type that suggests connections on the one hand with *Pithecanthropus* and on the other with the Neanderthal man of Europe (Fig. 501). *Sinanthropus* was lower browed than the Neanderthals, although in certain other respects the skulls are similar. It walked erect like a man, not on all fours like an ape. Two thighbones, although broken, indicate a possible height of 5 feet 4½ inches, which is a good human stature, especially since these may have been the bones of a woman. Animal fossils

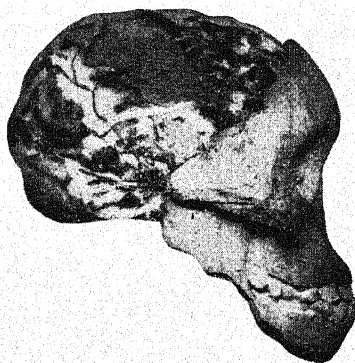


FIG. 498. The fossil of *Australopithecus africanus*, found at Taungs, South Africa (cf. Fig. 497 B). The shape and size of the brain is shown by material that filtered into the skull cavity and hardened into stone. The remainder of the skull was destroyed in the quarrying operations that unearthed the specimen (cf. Fig. 493).

(From R. Broom, 1925, *op. cit.*; courtesy of American Museum of Natural History and the author.)

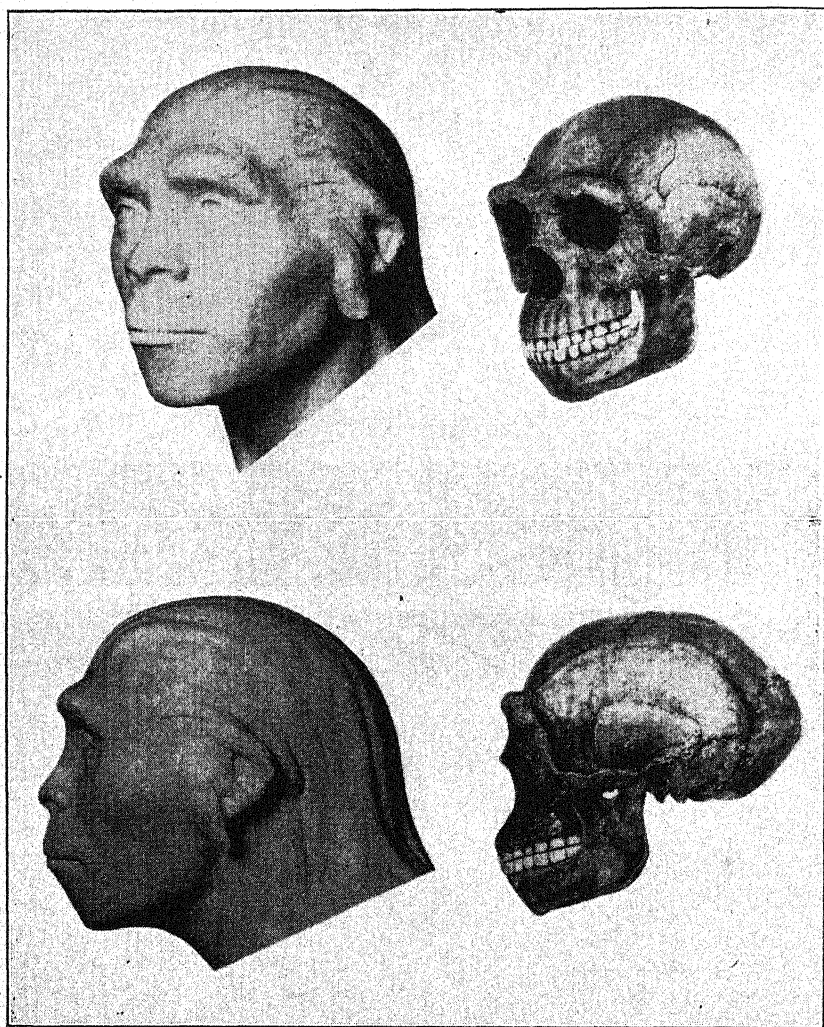


FIG. 499. Reconstruction of the Peking woman and skull on which this reconstruction was based.

(Courtesy of American Museum of Natural History.)

and artifacts found in the same caves with the Peking man's remains show that his race lived during early Glacial times, could fashion rough stone tools, and knew the use of fire. He was probably cannibalistic, since the skulls are broken and some of them seem to have been roasted.

Apparently man came upon the scene in Europe by migration from Asia or Africa during the early Pleistocene, one of the most dramatic

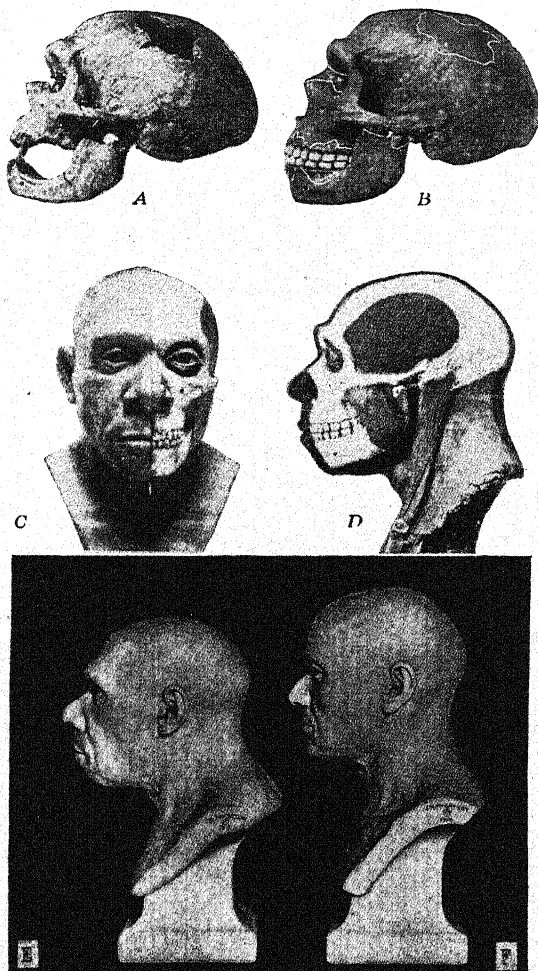


FIG. 500. Reconstruction of the flesh over a skull (cf. Figs. 493 and 501). *A*, skull of a member of the Neanderthal race found at La Chapelle-aux-Saints, France (from M. Boule). *B*, reconstruction of this skull with aid of other specimens showing the missing parts. *C* and *D*, addition of flesh after comparison of size of muscles, thickness of flesh, etc., in apes and man. *E*, the completed reconstruction of *A*. *F*, similar reconstruction of a man of Cro-Magnon, one of the prehistoric races of *Homo sapiens* with a brain capacity equal to that of modern man.

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epochs in the geologic history of the Northern Hemisphere. Glaciers slowly spread southward as they did in America, covering a large part of the continent not once but four separate times in Western Europe

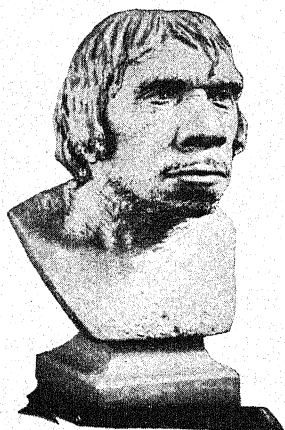


FIG. 501. The Neanderthal man, *Homo neanderthalensis*, restored by J. H. McGregor from the skull of La Chapelle-aux-Saints (cf. Figs. 493 and 500). This is the same bust as Fig. 500 E with the addition of hair and eyebrows, and a suggestion of beard not sufficient to obscure the form of chin. A few wrinkles were added and the iris and pupil incised so that their shadows might lend life to the eyes.

(Photograph by A. F. Heuttner, copyright by J. H. McGregor, reprinted by permission.)

during a period variously estimated as from 500,000 to 1,500,000 years. However, during the interglacial periods the climate was at times more equable than now. There were extensive forests even close to the ice, and the fauna included such mammals as the mastodon, the mammoth, the woolly rhinoceros, and the saber-toothed tiger. Man came as a puny competitor of these mighty animals but spread and flourished, to judge from the flint implements and the occasional skeletal remnants that enable us to picture the lives and nature of these primitive human beings.

The most widespread type among the ancient Europeans was the Neanderthal man, *Homo neanderthalensis* (Fig. 500 A-E), first discovered in the valley of this name near Düsseldorf, Germany, and now known by skeletal remains distributed from Gibraltar to the Crimea and Palestine. The much disputed Piltdown man of England, *Eoanthropus dawsoni* (Fig. 497 D), and the Heidelberg man of Germany, *Homo heidelbergensis*, were contemporaneous with early Neanderthals or preceded them. The Neanderthal men were succeeded by races of modern man, *Homo sapiens*, such as the men of Cro-Magnon (Fig. 500 F); and they in turn were displaced or absorbed by the progenitors of the modern Europeans. With the increased interest in all parts of the world discoveries are being

made at an accelerated pace, and wholly new finds may be reported at any time as well as additional fossils and artifacts of types already known. The early human types are already represented in sufficient diversity to suggest the origin of more than one species with human intelligence and the final survival of modern man alone. On the other hand, some anthropologists have argued in recent years that all these

types, from *Pithecanthropus* to the present-day races of mankind, should be included in the single species *Homo sapiens*.

In the Americas, the progenitors of the Indians, or *Amerindians*, were long believed to have reached the northern continent not earlier than several thousand years ago by migration across Bering Strait. Studies of burials and of skeletons found on some of the Aleutian Islands are making important additions to our knowledge concerning some of these aborigines. It is possible, however, that men have inhabited North

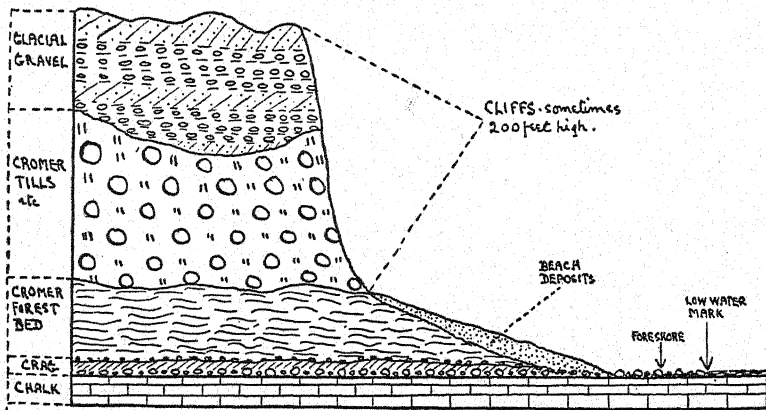


FIG. 502. Cliff and beach at Cromer, England, showing deposit called the crag, in which primitive flint implements are found (cf. Fig. 503). The age of the crag deposit is regarded by some geologists as Pliocene or late Tertiary (cf. Fig. 469). No skeletal remains of the manlike beings who made the implements have yet been found in this deposit.

(From J. R. Moir, 1924, *Natural History*, vol. 24; courtesy of American Museum of Natural History.)

America for a longer period. Among the earlier finds, suggesting that man has been in America longer than was thought, is that at Attica, New York, where pottery fragments were found in undisturbed clay beneath the skeleton of the extinct *Mastodon americanus*. In Logan County, Kansas, an arrowhead was found beneath the shoulder of the extinct *Bison antiquus*, as though it had been embedded in the flesh when the animal died. Near the town of Colorado, Texas, three large arrowheads of markedly different type from those of recent origin were found beneath the fossilized skeleton of a bison that was embedded in deposits of Pleistocene age. Associated fossil fragments in this Texas deposit show a fauna including mammoths, camels, and extinct horses. Finds in a gravel pit near Frederick, Oklahoma, were first brought to the attention of scientists in 1926. The artifacts, which include what are

claimed to be flat grinding stones and pestles, as well as arrowheads, were embedded in old river gravels at two distinct levels. The associated fossils include scattered bones of extinct animals, such as the mammoth, *Elephas columbi*, and at the lower levels the more primitive mammoth, *Trilophodon*; giant ground sloths; and three species of horses of the Genus *Equus*. These deposits were laid down so long ago that erosion by the present drainage system of the Red River has since cut to a level more than 250 feet below the gravel in question. Near Vero

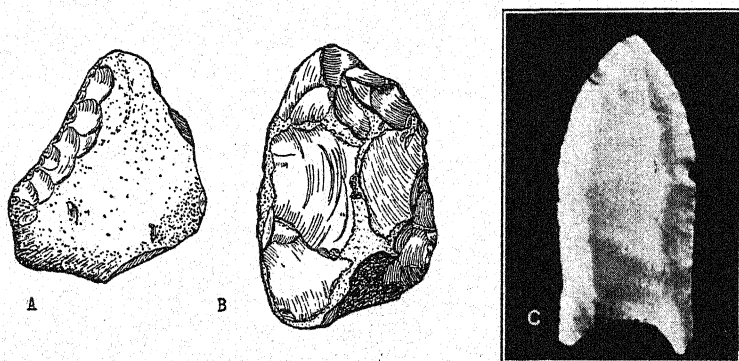


FIG. 503. Types of flint implements. *A*, an eolith or dawn-stone from Kent, England. *B*, an early paleolith or old-stone-age implement of Chellean type from the crag deposit (cf. Fig. 502). *C*, a Folsom point.

(*A* and *B*, from J. R. Moir, 1924, *Natural History*, vol. 24. All by courtesy of American Museum of Natural History.)

in Florida parts of human skeletons and artifacts seemingly associated with the bones of extinct forms, such as the mammoth, horse, and tapir, further indicate the coexistence of man with animals supposed to have become extinct in the Pleistocene. Again, in a cave near the Strait of Magellan artifacts have been found associated with the bones of the horse, the giant sloth, and other extinct species that were seemingly hunted by these early men.

Finds made in 1925 near Folsom, New Mexico, proved to be the most important of all these discoveries. Two points, probably small spear-heads rather than arrow points, were discovered in association with skeletons of an extinct species of bison. One of the points lay beside a rib in such a position that the animal probably died with the point embedded in its flesh. In this deposit the bison seem to have been killed by hunters at the edge of a lake and later trampled by other bison deep into the soft mud, which now appears as a tough clay silt cemented by lime. Since few tail vertebræ were found with the skeletons, it is

concluded that the Folsom hunters had skinned their quarry. Indeed, roughly made scrapers were found among the artifacts. Marks of flint knives were found upon some of the bones, and here and there a leg was missing as though cut away for roasting.

Folsomlike points (*cf.* Fig. 503 C) have since been found in such remote localities as Pennsylvania, New Jersey, Ohio and Mississippi. In

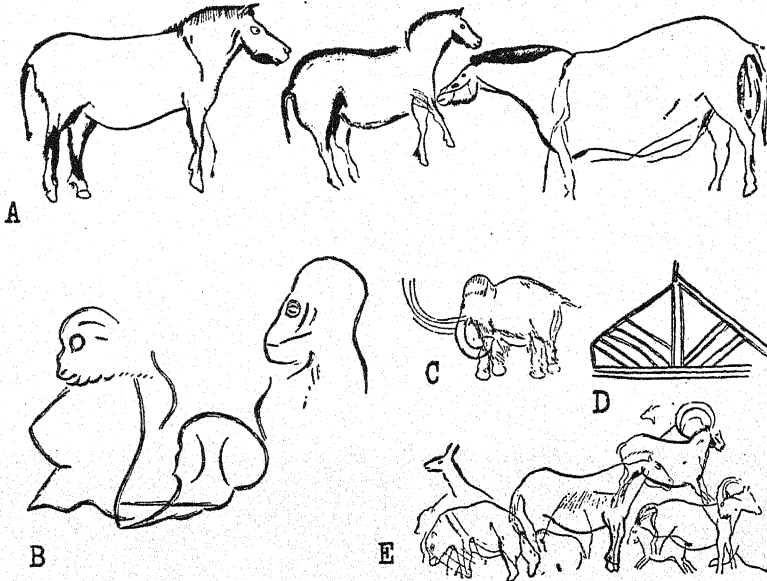


FIG. 504. Rock carvings from walls of cavern of Les Combanelles, France. A, group of horses. B, grotesque human heads or masks. C, mammoth. D, tectiform figure, perhaps representing a tent. E, group of animals.

(From H. Breuil, 1926, *Natural History*, vol. 26; courtesy of American Museum of Natural History.)

the Plains Region, the Lindenmeier site in eastern Colorado has revealed a camping place where Folsom hunters remained for a considerable time. Another camp site has been found at Clovis, New Mexico.

Most important is the finding of Folsom points at Chinitna Bay in Alaska, as marking the route of these early Americans from Asia to the new world. Folsom points are so distinctive that they are easily recognized, and they are prized by amateur collectors. Hence many casual finds have been reported. Apparently the Folsom hunters represent a culture preceding the earliest known cultures of recent American Indians. The deposits at Folsom are now dated as approximately 10,000 years of age. The culture was presumably widespread and of considerable duration. In northern Colorado it has been linked by geologists

with the retreat of the last glaciation, estimated at perhaps 20,000 years ago for that region.

During the third decade of this century another distinctive type of artifact began to be recognized. This was called the Yuma point because of its abundance near Yuma, Colorado. Whereas the Folsom points are from 1 to 3 inches in length, the Yuma points may be 6 or even 8 inches in length. Like Folsom points, they are superbly worked. Excavation of a camp site at Eden, Wyoming, has shown these Yuma points to be of much later origin than the Folsom type, although the Yuma man lived in America for many centuries.

The Folsom hunters of 10,000 or more years ago, however, were not the first Americans. Flints and camp sites have been found near Abilene, Texas, at considerable depths along the banks of streams. These may be older than the Folsom records. The bank of an arroyo near Cochise, Arizona, has yielded a record not of hunters but of "vegetarians." The layers in the Sandia Cave near Albuquerque, New Mexico, have revealed a record of the Folsom culture and, well beneath it, another culture dated at 25,000 years B.C. These earlier men of the Sandia Cave now stand as the earliest known Americans. They seem to have lived actually within the closing millennia of the last Ice Age.

The record has become increasingly complex through the finds of recent years. In the great basin between the Cascade Range and the Rocky Mountains there were extensive lakes in the early postglacial period. These lakes are now completely dried or are represented only by smaller bodies of water, such as Klamath Lake in Oregon. Artifacts found along the ancient shores of these lakes and in near-by caves have been dated as perhaps 15,000 years of age. Associated with these artifacts are the bones of extinct horses, *Equus*, and of camels. These and many other artifacts and camp sites associated with skeletal remains of extinct animals make it evident either that animals now extinct survived to a much later time than has been supposed or that men of some sort were upon the North American continent much earlier than any Amerindian migration of 4000 or 5000 years ago. It now seems probable that some of the extinct Pleistocene mammals survived until a more recent period than had been supposed. It is also probable that the earliest Amerindians reached North America via the Bering region, perhaps as early as 25,000 B.C., and were, no doubt, followed by succeeding waves of migration. The crucial point to determine is the geological age of the deposits in which the artifacts are found. Fortunately, it is sometimes possible to make such determinations of age within the postglacial period with considerable accuracy.

Thus, many artifacts and camp sites have been found, but at this writing there is only one skeleton claimed to represent the very early Amerindians, and the age of this skeleton is disputed. The "Minnesota man," or rather woman, was found in 1931 near Pelican Rapids, Minnesota, embedded in ground formed as the silt of a lake near the edge of the fourth glacial ice sheet as it retreated. Although the age of this deposit has been claimed to be perhaps 20,000 years, some American anthropologists contend that the skeleton found its way into the deposit by a comparatively recent and artificial burial. The Minnesota skeleton is, in fact, much like the skeletons of the Indians who recently inhabited the region. Whatever may be the truth in this case, it is not to be expected that the skeletons of the earliest Amerindians, when they are found, will differ greatly from the present types. Modern man must have been well established in northeast Asia much earlier than 25,000 years ago. There is abundant evidence that the earliest Amerindians came from this mongoloid stock as did the Amerindians of subsequent migrations in the Alaskan region.

THEORIES CONCERNING ORGANIC EVOLUTION

Organic evolution as an historic fact is attested by the evidence outlined in the preceding section. We may now examine the more important theories concerning the factors that condition such evolution. Notable among these formulations are the Lamarckian Theory of the Inheritance of Acquired Characters, the Darwinian Theory of Natural Selection, the Mutation Theory of de Vries, theories of Orthogenesis, Isolation, and Hybridization, and the conclusions from recent studies in genetics and in ecology. To be comprehensive any theory must include both internal and external factors. As examples of internal factors may be cited the phenomena of heredity, variation, reproduction, and development; as examples of external factors, any environmental conditions that profoundly affect individuals and populations.

The Lamarckian Theory of the Inheritance of Acquired Characters

Historical. Evolutionary changes conditioned by the inheritance of characters acquired during the life of the individual were postulated in the works of Lamarck (1744-1829), written principally during the first quarter of the nineteenth century (Fig. 505). Another Frenchman, Buffon (1707-1788), had previously stated the concept of evolution as opposed to special creation, and Lamarck built upon this foun-

dation (Fig. 506). Many of Lamarck's statements are fanciful in the light of modern knowledge. Even his essential claim that characters acquired by an individual in its lifetime are inherited by its offspring and thus produce evolutionary changes now seems ridiculous to many biologists, although it is still championed by those who accept the Lamarckian Theory of today.

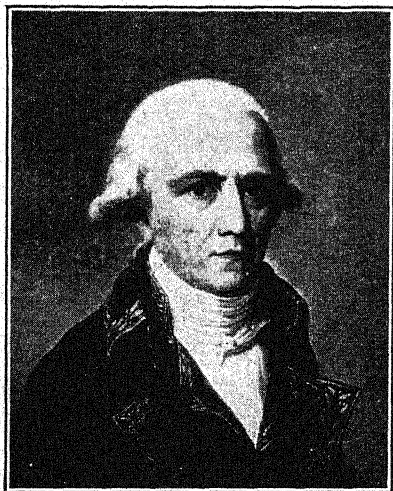


FIG. 505. Jean Baptiste de Lamarck (1744-1829), first to propose a theory of the factors of organic evolution that received serious consideration.

(From L. V. Pirsson and C. Schuchert, "Textbook of geology," copyright, 1924, by John Wiley and Sons, reprinted by permission.)



FIG. 506. Georges Buffon (1707-1788), scientist and popular writer, who has not received due credit as an early advocate of organic evolution.

(From W. A. Locy, "Biology and its makers," copyright, 1908, by Henry Holt and Co., reprinted by permission.)

Explanation of Lamarck's Theory. In its modern form the Lamarckian Theory states that during the life of an individual new characters can be acquired by use and disuse and also by the direct effects of the environment on the somatic cells. It is a familiar fact that the use of muscles increases their development. The old adage "practice makes perfect" finds many illustrations in the neuro-muscular coördinations that are perfected by use. Conversely, disuse leads to deficiency or even complete loss of function, as is illustrated by the fanatic of India who holds a limb in one position until it cannot be moved. A white man who lives for years in the tropics may acquire a sunburn that is recognizable long after his return to a temperate

climate. Horses kept in mines and men kept in dungeons are said to have had their eyes so impaired that they could be restored to sight only by gradual exposure to light, if at all. Such examples of the effects of use and disuse and of environment are known technically as *acquired characters*. It is further stated by the Lamarckian Theory that characters thus acquired in an individual are inherited by its offspring (*cf.* Fig. 507 Below).

The process that is supposed to occur in nature may be illustrated by citing some of Lamarck's own examples in modern terms. If swift-footed animals, such as deer, have acquired their fleetness by running from their enemies, it follows that each generation has been forced to exert itself to the utmost, like an athlete always in training for a race, and that the effects of the training in each generation have been passed on to the next. Thus, fleetness has gradually increased up to limits determined by the nature of the organism. In like manner, the fleetness of the pursuing wolves may have been increased generation after generation. If cunning were practiced, the more effective use of the brain would be fostered and any gain in efficiency passed on to the descendants. Animals living in caves cease to use their eyes, and the degeneration that follows is supposed to be cumulatively inherited until blind species are produced. Animals living in cold climates, where the environment stimulates a heavier growth of hair or the formation of more fat beneath the skin, are believed to transmit these characters by heredity and thus to reach the state seen in Arctic forms. The giraffe is supposed to have stretched its neck by reaching into the trees for its food, and so each generation to have inherited a slightly greater length of neck until the present state was attained (Fig. 507 Above). Lamarck also thought that the animal in some way "willed," or determined, the course of its evolution.

Status of Lamarck's Theory. There would be little criticism of the Lamarckian Theory if it could be shown that the effects of use and disuse and the direct effects of environment upon the individual are actually inherited. If this inheritance does not occur, there is no evolutionary change, because each generation starts on the same level as its parent. Many attempts have been made to obtain specific evidence, but none of the alleged examples has withstood the attacks of subsequent investigation. If the theory is correct, satisfactory evidence should be forthcoming. Lamarckians no longer believe that disuse after mutilation causes hereditary degeneration. As one writer puts it, "Wooden legs do not run in families, although wooden heads may." Experiments in the destruction of parts, such as the amputation of tails in mice during many generations, in the functional stimulation of cer-

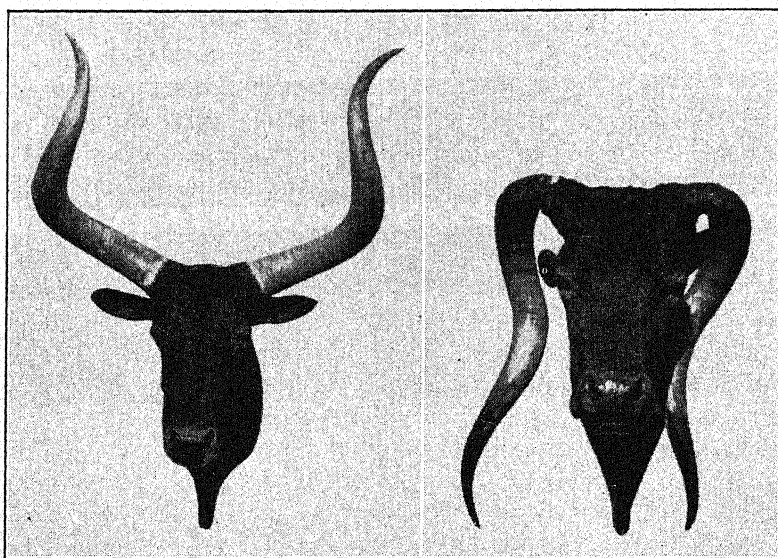
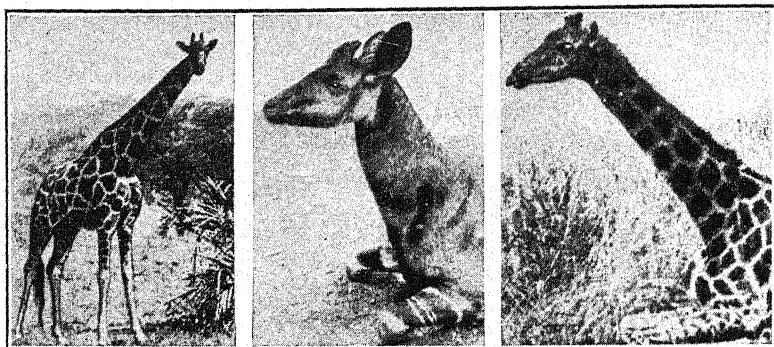


FIG. 507. Effects of use and of environment, in relation to the Lamarckian theory. *Above*, the familiar long-necked giraffe (*left and right*), which lives upon the savannas of Africa and browses upon the higher branches of trees; and the okapi, or forest giraffe (*center*), which browses upon lower branches. *Below-left*, mounted head of a normal Texas longhorn steer; and (*below-right*) the head of a longhorn with drooping horns, caused by lack of phosphorus and calcium in the diet. The Lamarckian would claim that the elongated neck of the giraffe represents inheritance of the effects of use, and that such an environmental effect as the drooping horns of the steer might be inherited.

(*Above*, photographs by courtesy of American Museum of Natural History. *Below*, photographs from an exhibit in the W. D. Rock Museum; courtesy of the Museum.)

tain parts, and in the effects of changed environment, have given results that are considered negative by most investigators. The organism may develop new characters in a new environment, but, when it is returned to the original environment, these changes are not lasting.

It is true that during the past 50 years various investigators have proclaimed experimental results supporting the theory. The conclusions drawn from these studies, however, have been shown one after the other to be incorrect or to be explicable in some other manner. They have not met the test of being obtained by subsequent investigators, as must scientific conclusions that become firmly established. Experimentation thus fails to support the Lamarckian Theory, since it appears that characters acquired by the individual in the manner indicated are not inherited.

A theoretical objection can be based upon the mechanism of such inheritance, if it be assumed to occur. An individual develops not from its parents' somatic cells but from the parents' germ cells, which seem in many instances to be set apart at an early stage in development and to be little influenced by what happens to the somatic cells in the normal activities of the animal (*cf.* p. 114). If the Lamarckian scheme holds, one must suppose that a change in a given part of an animal is transferred to the germ cells in such a way as to affect whatever it is in the germinal material that conditions the development of this part. A blacksmith's son inherits his arms not from his father's arms but through his father's and mother's germ cells, and the germ cells of the father must be changed before any modification can be inherited. The facts of genetics, embryology, and physiology give virtually no theoretical support to the Lamarckian doctrines and thus confirm the negative results obtained from experimentation. It should be said, however, that a limited number of zoölogists regard some of the modern experimental evidence for Lamarckism more favorably than is indicated by the foregoing statements. The problem is a complex one, and it is conceivable that evidence for the inheritance of characters acquired by use or disuse and by the direct influence of environment upon the somatic cells may yet be discovered. The old Scotch verdict of "not proven" is a good one in a case of this sort, although the long-continued failure to secure evidence for the inheritance of such characters counts heavily against the theory.

The Darwinian Theory of Natural Selection

Historical. The teachings of Lamarck regarding evolution attained considerable vogue during the early nineteenth century but were ap-

parently overthrown by Cuvier (1769–1832), the greatest zoölogist of his day, who opposed the concept of evolution (Fig. 470). In 1830, the year after Lamarck's death, a debate was held before the French Academy in which Saint-Hilaire (1772–1844) upheld the Lamarckian doctrines against Cuvier. Although Cuvier was not an evolutionist, he

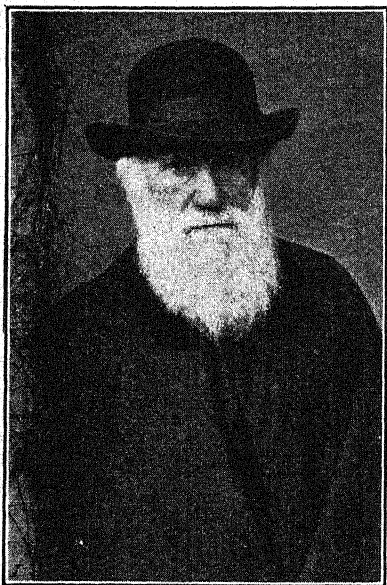


FIG. 508. Charles Darwin (1809–1882), first to collect and present data that established the fact of organic evolution, and who proposed Natural Selection as a factor in such evolution.

(From F. Darwin, "The life and letters of Charles Darwin," D. Appleton and Co., copyright, 1899, reprinted by permission.)

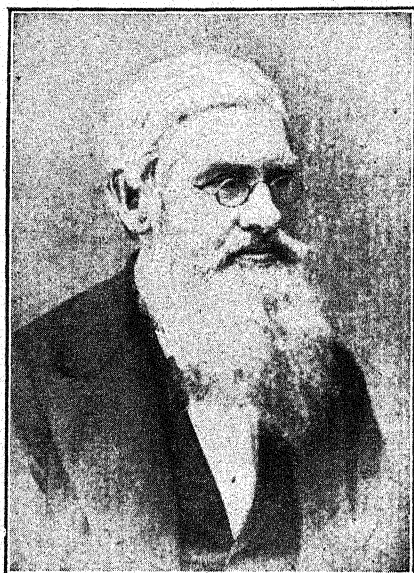


FIG. 509. Alfred Russel Wallace (1823–1913), who also proposed Natural Selection as a factor in organic evolution and who was a lifelong friend of Darwin and supporter of his views.

(From L. V. Pirsson and C. Schuchert, "Textbook of geology," John Wiley and Sons, copyright, 1924, reprinted by permission.)

had been forced to admit the differences between animals of the past and those of the present, a difference which could not exist if animals were originally created as they are now and had not changed. Accordingly, he had espoused the Doctrine of Cataclysms, which assumed not one but a series of creations, each followed by a cataclysm that destroyed all life. By supposing that each creation was on a higher level than the preceding one, it was possible to explain the succession of types appearing in the fossil record. But the work of geologists, begun in the latter part of the eighteenth century and culminating in 1830 with

Lyell's "Principles of geology," showed that there had been no cataclysms. The period from 1830 to 1859, during which Darwin was engaged in the studies summarized in his book "The origin of species," was one of quiescence for the evolutionary theory. However, there was much popular interest in the subject, as shown by the large sales of Robert Chambers' book, "The vestiges of creation" (1844), to which due credit has not been given by historians of evolution. Cuvier won his debate with Saint-Hilaire, but in 1830 the case was already settled in favor of evolution, as subsequent developments showed.

Charles Darwin (1809-1882) began his work 20 years before the publication of his famous volume (Fig. 508). The fact that he was interested in determining whether species originated by creation or by transmutation, that is, by evolution, shows that the question was then under discussion. The idea of evolution seemed new in 1859 only because the evidence was so ably presented by Darwin and so rapidly accepted by scientists and others. It is rather discreditable to biologists that they failed to recognize at an earlier date the evidence for organic evolution that had been steadily accumulating since the work of Buffon (1749) and that was sufficient to justify acceptance of the concept 20 years before 1859. Nevertheless, Darwin deserves the place he occupies, because he brought about the acceptance of evolution. His "Origin of species" was a masterful extension and summary of the evidence for organic evolution as an historic fact. Its publication marked the beginning of a new epoch in human thinking as well as in biological science.

Explanation of Darwin's Theory. In addition to bringing together and extending the evidence for the fact of organic evolution, Darwin proposed as the major factor in the origin of species, and hence of evolution, what he called *natural selection*, the principles of which were independently recognized in 1858 by Alfred Russel Wallace (Fig. 509).

Proved Facts	Consequences
A. Rapid Increase of Numbers B. Total Numbers Stationary	Struggle for Existence
C. Struggle for Existence D. Variation and Heredity	Survival of the Fittest (Natural Selection)
E. Survival of the Fittest F. Change of Environment	Structural Modifications

FIG. 510. Wallace's chart of natural selection.

As outlined by Wallace, the process of natural selection operates in the manner shown by Wallace's Chart (Fig. 510) and explained in the following paragraphs.

Capacity for Rapid Increase in Numbers. In all forms of life there is an ever-present capacity for rapid increase, which is shown by theoretical calculations of the potential rate of multiplication.

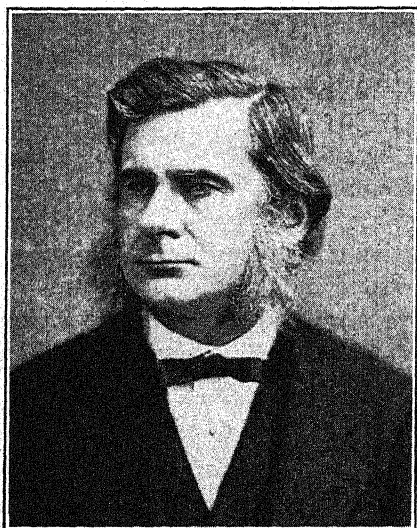


FIG. 511. Thomas Henry Huxley (1825-1895), comparative anatomist, paleontologist, and effective popular advocate of organic evolution in the decades after the publication of Darwin's "Origin of species."

(From L. V. Pirsson and C. Schuchert, "Textbook of geology," John Wiley and Sons, copyright, 1924, reprinted by permission.)

A single pair of elephants, among the animals cited by Darwin as slow breeders, would have at the end of 750 years nearly 19,000,000 descendants, if all the individuals lived 90 years and each female gave birth to six young. For the American oyster, which may produce as many as 60,000,000 eggs annually, the following calculation has been made. If a single oyster produced 16,000,000 eggs, all of which were fertilized and came to maturity, and if half of these became females and went on increasing at the same rate, there would be in the third generation 64 millions of millions of females and in the fifth generation 33,000 millions of millions of millions of millions of females. If to these were added an equal number of males, the bulk of the shells would then be more than eight times that of the earth.

Again, in his pedigreed cultures of *Paramecium*, L. L. Woodruff calculated that the number of cells produced in 3029 generations, during a period of 5 years, would be represented by 2 raised to the 3029th power, and that the volume of protoplasm would not be less than 10^{1000} times the volume of the earth. Similar potentialities exist in all animals and plants.

Evidence that very rapid increase can actually occur is seen when animals and plants spread over new territory that is suited to their needs. The English sparrow was first imported into the United States about 1850. Within 25 years it had spread and become a pest. It is

now our most abundant and widely distributed bird. The European starling, apparently originating from an importation into Central Park, New York City, in 1890-1891, is another example (Fig. 513). The German carp was introduced into the United States by importation of small numbers. In the Mississippi Valley alone it has now spread into almost every stream that affords a suitable environment. The

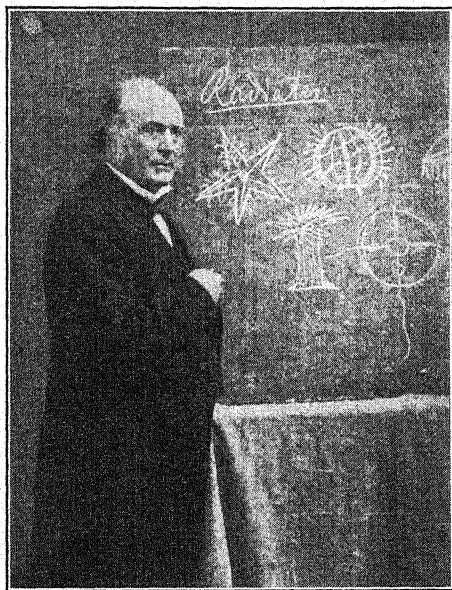


FIG. 512. Louis Agassiz (1807-1873), pupil of Cuvier and distinguished Swiss zoölogist, later professor at Harvard University. Unlike Huxley and Wallace, Agassiz was unable to appreciate the evidence for organic evolution, although his own studies often present this evidence in a striking manner (*cf.* Fig. 486, A to C).

rabbits that have overrun Australia were introduced there and rapidly increased. The same is true of the herds of wild horses that were abundant in North and South America in the early nineteenth century. Other examples of actual increase that approximates the theoretical possibilities are seen in the plagues of insects and other small animals which occur in years when conditions are favorable for the development of an unusual percentage of the eggs. We may, therefore, conclude that the capacity for rapid increase in numbers is always present.

Total Numbers Remain Stationary. Despite the potentialities of increase it is evident that the total numbers of any species in nature must remain approximately stationary save for the annual fluctuations

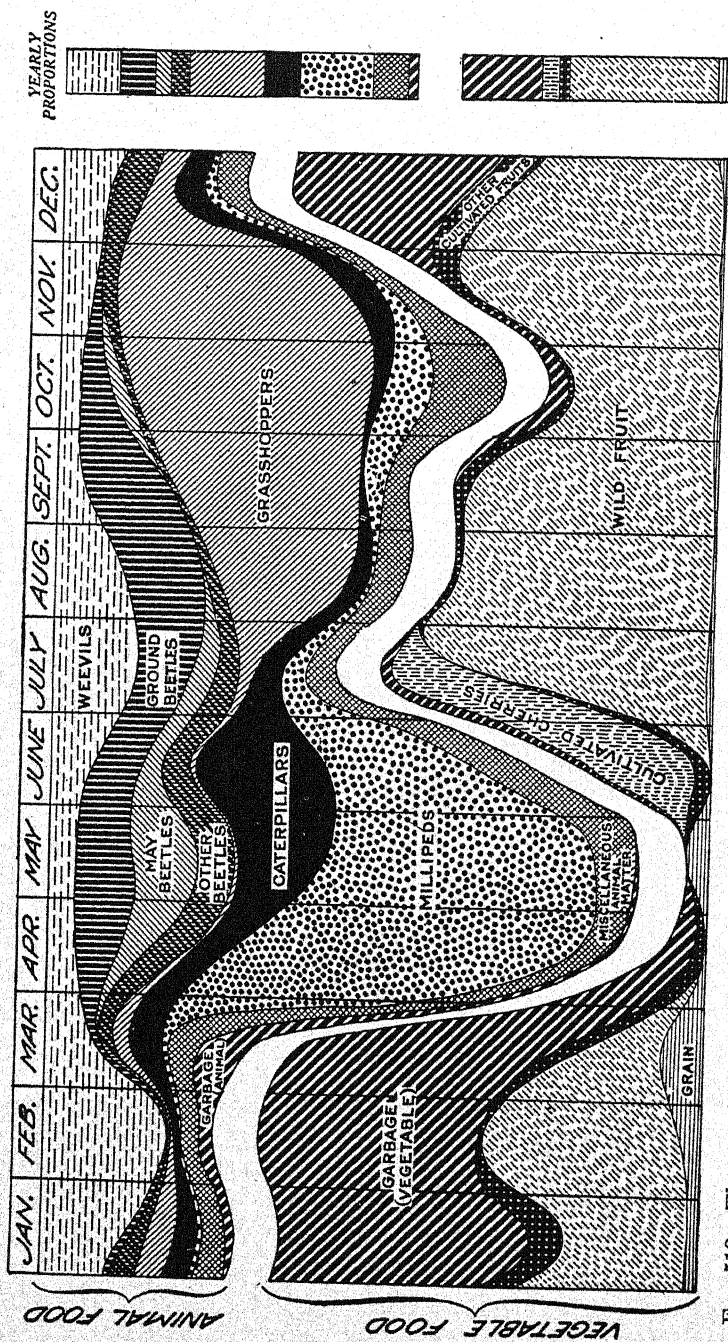


FIG. 513. The starling, *Sturnus vulgaris*: The diversified food of this invader is doubtless a factor in its establishment and in the rapid extension of its range upon the North American continent (Continued, p. 701).

due to varying conditions and the occasional expansions when new territory is invaded or when some change of the environment provides an opportunity for expansion. Numbers are held stationary by what

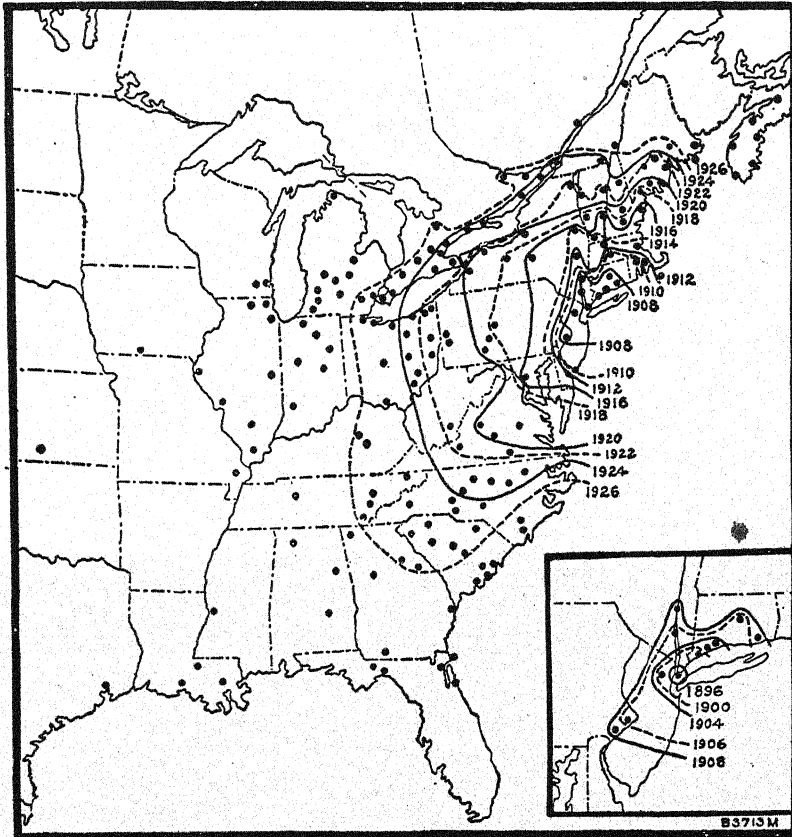


FIG. 513. The starling (*Concluded*): Since the date of this census the bird has substantially extended its range; it is now common in some regions where it had not been reported in 1926. Areas successively covered in two-year periods are shown by alternating broken and continuous lines. Spots outside the line of 1926 indicate isolated records, mainly in winter.

(From E. R. Kalmbach, 1928, *Farmers' Bulletin*, No. 1571, U. S. Dept. Agriculture.)

Darwin called the checks upon increase. These are often complex, involving interrelationships among different species. One of the many examples cited by Darwin is as follows:

"I have also found that the visits of bees are necessary for the fertilization of some kinds of clover; for instance, 20 heads of Dutch clover (*Trifolium repens*) yielded 2,290 seeds, but 20 other heads pro-

tected from bees produced not one. Again, 100 heads of red clover (*T. pratense*) produced 2,700 seeds, but the same number of protected heads produced not a single seed. Humble-bees alone visit red clover, as other bees cannot reach the nectar. It has been suggested that moths may fertilize the clovers; but I doubt whether they could do so in the case of red clover, from their weight not being sufficient to depress the wing petals. Hence we may infer as highly probable that, if the whole genus of humble-bees became extinct or very rare in England, the heartsease and red clover would become very rare, or wholly disappear. The number of humble-bees in any district depends in a great measure upon the number of field-mice, which destroy their combs and nests; and Col. Newman, who has long attended to the habits of humble-bees, believes that 'More than two-thirds of them are thus destroyed all over England.' Now the number of mice is largely dependent, as every one knows, on the number of cats; and Col. Newman says, 'Near villages and small towns I have found nests of humble-bees more numerous than elsewhere, which I attribute to the number of cats that destroy the mice.' Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district."²

In examining such chains of events, one should remember that a chain is no stronger than its weakest link. If one link breaks, the conclusion does not follow from the premises. It is quite possible that the foregoing relationship between cats and clover may not obtain, because one or more links of the sequence do not exist. Probably in no example like this, when observed in nature, can one be sure that the relationships assumed are in reality matters of life and death in a large number of cases. Nevertheless, the many glimpses of such relationships that are disclosed indicate that living beings are frequently interrelated in ways of the utmost importance to the organisms concerned and that interdependence of organisms is one of the major factors in the complex of animate nature.

Figure 514 illustrates how these intricate interrelationships between organisms are analyzed by the ecologist. The author of this figure writes:

"Any marked fluctuation of conditions is sufficient to disturb the balance of an animal community. Let us assume that because of some unfavorable conditions in a pond during their breeding period the black bass decreased markedly. The pickerel, which devour young bass, must

² From Charles Darwin, 1859, "Origin of species," pp. 90-91, D. Appleton and Company, 1897.

feed more exclusively upon insects. The decreased number of black bass would relieve the drain upon the crayfishes, which are eaten by bass; crayfishes would accordingly increase and prey more heavily upon the aquatic insects. This combined attack of pickerel and crayfishes would cause insects to decrease and the number of pickerel would fall away because of the decreased food supply. Meanwhile the bullheads, which are general feeders and which devour aquatic insects, might feed

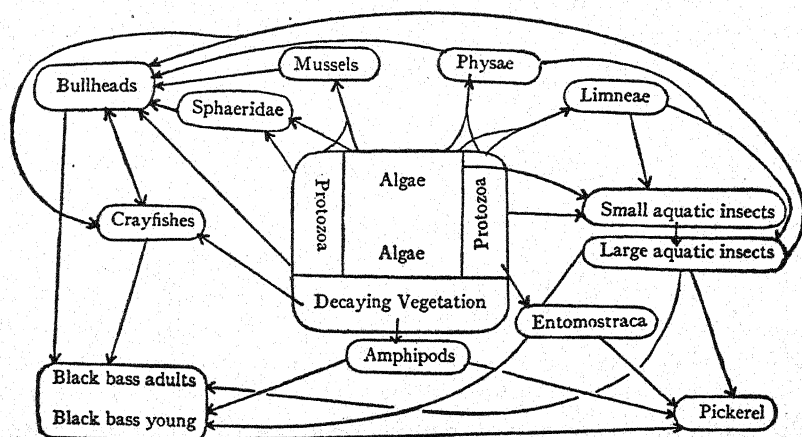


FIG. 514. Equilibrium in food relations of a pond community. Modern ecologists in ecology have emphasized further the intricacies of the interrelationships between organisms that were recognized by Darwin in the formulation of his Theory of Natural Selection.

(From V. E. Shelford, "Animal communities in temperate America," copyright, 1913, by Geographic Society of Chicago, reprinted by permission.)

more extensively upon mollusks because of the decrease of the former, but would probably decrease also because of the falling-off of their main article of food. We may thus reasonably assume that the black bass would recover its numbers because of the decrease of pickerel and bullheads, the enemies of its young. A further study of the diagram shows that a balance between the numbers of the various groups of the community would soon result. Under other circumstances, such as the extinction of the black bass, the resulting condition would be entirely different from the original one, but a balance between supply and demand would nevertheless finally be established."³

Food and space are the ultimate checks, although others usually intervene before these can become operative. For example, there is

³ From V. E. Shelford, "Animal communities in temperate America," copyright, 1913, by Geographic Society of Chicago, reprinted by permission.

plenty of food for herbivorous animals during the greater part of the year; their numbers are limited not by the food supply but by the carnivorous animals that prey upon them. Parasites play a rôle similar to that of predatory enemies, and climatic and seasonal conditions may also act as checks while the food supply is still abundant. So effective are the checks in their collective action that the abundance of adult individuals in any species is not so much a matter of the eggs or young produced as of the chances for destruction. As Darwin said, "The condor lays a couple of eggs, the ostrich a score, and yet in the same country the condor may be the more numerous of the two; the fulmar petrel lays but one egg, yet it is believed to be the most numerous bird in the world." Again, "One fly deposits hundreds of eggs, and another, like the hippobosca, a single one; but this difference does not determine how many individuals of the two species can be supported in a district. It would suffice to keep up the full numbers of a tree, which lived a thousand years, if a single seed were produced once in a thousand years, supposing that the seed were produced and never destroyed and could be ensured to grow and germinate. Lighten any check, mitigate the destruction ever so little, and the number of the species will almost instantaneously increase to any amount."

The Struggle for Existence. Since the capacity for reproduction is thus restricted by the checks upon increase, relatively few of the individuals that begin life in any generation will reach maturity. It is, therefore, concluded that there must be a *struggle for existence*. As Darwin conceived it, this struggle is seldom an actual conflict, although it may be when animals fight with one another for food or mates. He thought the struggle would be most acute between individuals of the same species, since these compete for the same conditions of life, or between widely different species using the same food, as when insects devour the food of grazing mammals. Another example of a struggle involving individuals of quite different species would be the hunting of herbivorous animals by carnivorous enemies. For example, wolves struggle for their existence when they pursue deer, and deer in turn struggle to escape from their pursuers. In certain species, such as the fur-seal, the struggle becomes an actual combat when the males fight for possession of the females. Finally, there is the struggle with the physical factors of the environment, heat and cold, moisture and dryness, a changing climate, change of the land surface, change of bottom conditions in the ocean or in fresh water. The struggle is, therefore, threefold—for food, for mates, and against fate.

It is important to bear in mind that Darwin thus used the term struggle in a general and metaphorical sense. In the vast majority of

cases there is nothing that can be called a struggle in the sense of an actual combat. Metamorphically, however, it can be said that the trees of a forest "struggle" to exist or "fight" for life. Darwin concluded that such a struggle, in one or more of its aspects, is ever-recurring for all organisms, although it is intermittent and may not act for considerable periods in the life of any individual. Because it seems a necessary consequence of the limitation of numbers in the face of great overproduction, the struggle for existence is transferred to the column of proved facts, as Figure 510 indicates.

Variation, Heredity, and Natural Selection. The modern concepts of variation and heredity have been presented in Chapter 6. Heredity has been defined as the tendency of individuals to resemble their ancestors and relatives, and variation as the tendency of individuals which are related by descent to differ in diverse ways (p. 160). The two are intimately connected as different expressions of the reproductive and developmental processes. Darwin observed that the members of species varied, and he believed that many of these variations, small though they might be in many instances, were inherited. He was interested in heredity and variation as such and studied them extensively. But so far as they concerned natural selection, it was not necessary to explain them. His argument was: given heritable variations and the reproductive capacities of organisms, a struggle for existence and natural selection inevitably follow.

With inherited variations of many sorts, some will be of value to the individual in its struggle for existence; that is, some will have *survival value*. According to Darwin, if the members of a species of plant varied in their ability to resist frost, those that were sufficiently resistant would survive a temperature that would be fatal to the great majority. Inheritance of the variation by the next generation would follow, and such a process of selection repeated generation after generation would result in a population better fitted to meet this necessity of its existence. Thus, evolution might occur by modification of this particular feature of the organism in a manner to suit a changing climate or to enable the species to extend its range northward. If rabbits differed in quickness of start and in sustained speed, and if these differences were important in escaping enemies, the quickest and speediest in each generation would tend to survive; and thus a race having greater speed would gradually come into existence. In like manner heritable differences in resistance to a disease would result in a more resistant race. If wits were more important than strength, selection would develop a more cunning type. If concealment were of life-and-death value, coloration and other features that tend to make the indi-

vidual resemble its surroundings would be at a premium and therefore selected. Darwin called the process by which useful variations were sorted out *natural selection*, because of its resemblance to the *artificial selection* used by breeders of animals and plants in picking individuals that pleased the fancies or the necessities of man (*cf.* p. 672). Herbert Spencer called the process *survival of the fittest*, since the individuals best fitted to the conditions of life were the ones to survive. In terms of genetics the rate and extent of any evolution thus directed by selection depend upon the occurrence of *heritable variations* that can be selected. Fluctuations are of no importance, since they are not inherited (*cf.* p. 164). Also, the distinction must be recognized between selection of lines already existent in a population, as shown by Johannsen (*cf.* p. 163), and selection of heritable variations that arise *de novo*.

Change of Environment. The environment has been referred to as though it were constant. Yet great changes take place over long periods of time, as when continents are made and unmade by geologic evolution, or profound climatic changes occur, such as the advent of an Ice Age or the change from forest to desert conditions. These are probably less important than changes of environment that may seem insignificant (*cf.* Fig. 514). The introduction or destruction of a plant upon which various animals feed may produce far-reaching changes in the environmental conditions of a given species. New enemies entering a district may bring new standards of selection; new parasites or disease-producing organisms may put a premium upon qualities that have not been hitherto selected. In the interplay of forces it is possible that conditions, and therefore selection, may remain stable for long periods, or that selection may suddenly take new directions. Changes of many sorts are thus conceivable within the limits of the selection pressure and the heritable characters available for selection. In terms of natural selection the environment may be compared to a sieve that selects the individuals presented to it but does not determine their nature. As long as the sieve remains unchanged, it allows the same kind of individual to pass its meshes, that is, to survive; but the sieve may change and may then select new kinds of individuals for survival. Evolution now in one direction and now in another is, therefore, possible.

In conclusion, it should be reiterated that the theory of natural selection does not attempt to explain the nature of variation and heredity. Selection is a directive rather than a creative factor in evolution. Neither does selection attempt to explain the evolution of non-adaptive, that is, of non-useful characters, unless they are linked in heredity with characters that are adaptive.

Status of Darwin's Theory. Despite the masterful presentation of fact and argument by Darwin in support of natural selection as a factor conditioning evolution, criticism of the theory was not lacking in the decades after 1859, and this criticism increased toward the end of the century. With the scanty knowledge of heredity and variation before 1900 little could be added to what Darwin knew concerning these phenomena, except the statistical data of Galton (*cf.* p. 161) and his followers and the insistence of Weismann that germ plasm rather than somatoplasm was important for heredity. The reality of a struggle for existence and hence the selection of heritable variations was seriously questioned, because the struggle could be recognized only in its general aspects from bits of detail here and there. As Darwin wrote, "Battle within battle must be continually recurring with varying success," yet we can see only fragments of the picture. "All that we can do, is to keep steadily in mind that each organic being is striving to increase in a geometric ratio; that each at some period of its life, during some season of the year, during each generation or at intervals, has to struggle for life and to suffer great destruction." In the 40 years that followed 1859 no biological topic was more discussed than natural selection, but there was virtually no persistent investigation by the methods of observation and experiment, so much used by Darwin, of the evidence for such a selective process in nature. Today, genetics has clarified the phenomena of heredity and variation with reference to natural selection, and ecology has greatly extended our knowledge of conditions in nature and made a beginning of experimentation. More recently, the intensive study of problems related to the struggle for existence and to populations has yielded significant data.

From genetics it is clear that fluctuations, which are not inherited, can be distinguished from the heritable variations which alone can be significant for the selective process. Changes in the genic make-up and hence the adult characteristics of any population constitute evolution, and the major evolutionary changes of the past must be interpreted through understanding of the minor changes observable at the present time. The definition of a species that has been so difficult in terms of a fixed unit of population is solved, unless it is made even more difficult, by defining a species as "a stage in a process" of evolution. Given heritable variations as the outcome of hybrid combinations, chromosomal aberrations, and mutations, the evolutionary process becomes a problem in the survival of certain gene complexes, as expressed in the characteristics of individuals, within a given population. Among the factors that condition survival and thus direct evolution, it appears that various form of *isolation*, such as the geographical isolation of groups,

which has long been recognized, and particularly their physiological isolation in breeding and otherwise, are of great importance in relation to the initial establishment within species of lesser populations that may eventually be subject to natural selection.

From ecology increasing knowledge of the struggle for existence has been secured. Studies of plant communities, such as forests, swamps, and meadows, have shown the conditions of competition and survival for individuals of the same and of different species in nature. Experimental tree-plantings in forestry and horticulture and plantings of forms, such as the dandelion, have shown the manner of competition and survival under various conditions. Although these multitudinous investigations have greatly extended our knowledge of plant populations and incidentally of the related animal life, they have had one limitation. They have dealt mainly with the growth of single generations. The evolutionary process involves a succession of generations and the changing characteristics of their individuals. Study of animal communities has yielded similar data (Figs. 514 and 518), and in recent years attention has been directed to successive generations in particular environments. The complexities of the relationships in nature are increasingly evident, but progress can be made by focusing attention upon an aspect of the problem, such as the growth of populations in relation to food supply and other conditions, the relationships between species in mixed populations, and the predator-prey relationship. Since these conditions are well-nigh impossible to determine precisely for the larger animals in a state of nature, investigators have had recourse to laboratory experiments with smaller forms.

For example, the experimental study of population growth in various organisms, such as the fruit-fly *Drosophila* and various unicellular forms (Fig. 515), shows this growth to follow what has been called the *logistic curve*, which can be expressed in mathematical terms. This seems to be a universal law of population growth applicable from yeast cells to man. A saturation level is reached when the opportunity for growth has been fully realized in a given environment, although this level may be raised or lowered by a change in the environment. Thus in a protozoan culture the population may become stabilized at a certain level but can be advanced by increasing the food supply. In western Europe the human populations, which had been held at low levels through the Middle Ages, were raised to higher levels when the centuries of discovery and increasing wealth, followed by advances in the use of machines, in agriculture, and in medical science, made possible the maintenance of much larger populations in given areas. In the United

States today, the logistic curve, after a sharp rise during the nineteenth century, shows signs of flattening so that the biometricians prophesy a level of saturation and hence a limit to population growth within a few decades.

Having such a general law of population growth, one can examine the factors that determine population levels in specific cases. With yeast plants in pure culture, it is found that production of a certain

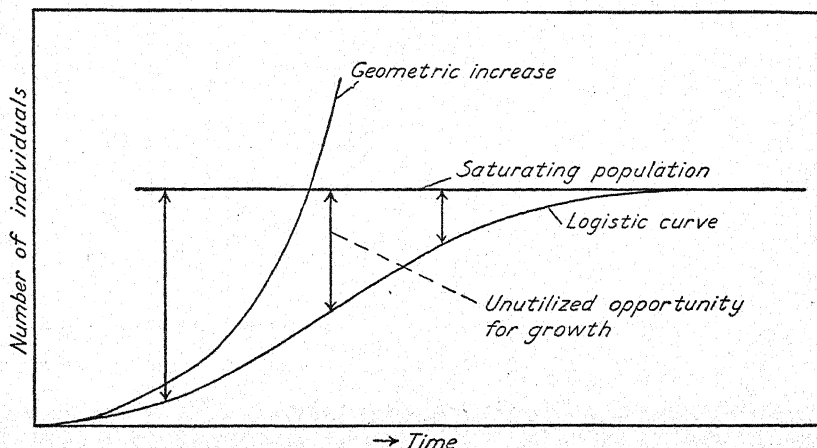


FIG. 515. The curve of geometric increase, which represents the theoretical possibilities, and the logistic curve, which represents the actual rate of growth in animal populations.

(Redrawn from G. F. Gause, "The struggle for existence," copyright, 1934, Williams and Wilkins, reprinted by permission.)

percentage of alcohol and not available food supply is the limiting factor. When the two species of protozoans *Paramecium aurelia* and *Stylonychia pustulata* are cultivated together, they first compete for the available food supply, but eventually *Paramecium* survives and *Stylonychia* disappears (Fig. 516). When *Didinium nasutum* is introduced into a sedimentless culture of *Paramecium caudatum* (Fig. 517 and cf. Fig. 180, p. 271), the *Didinium* multiplies until it devours all the *Paramecium*, after which the *Didinium* dies out. When sediment is added to the culture, the *Didinium* multiplies to some extent and then dies out, whereas the *Paramecium*, some of which have always been protected by the sediment, are found to survive the predator and to flourish again with its extinction. To imitate another possibility in nature, "immigrations" of *Didinium* can be arranged, with the result that the two populations rise and fall in relation to one another.

The significance of these studies is that specific interactions in the struggle for existence are being isolated for examination. Principles so established can presumably be extended to the interpretation of cases, such as prey-predator relationships between two mammals, where it would be impossible to set up exact experiments. Similar procedure in other fields has yielded results of great importance, as with Mendel's

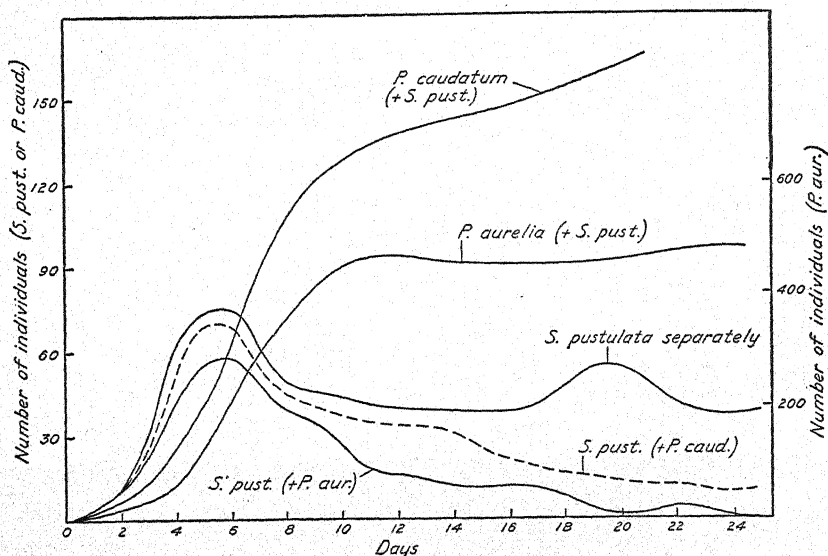


FIG. 516. Increase in number of individuals of *Stylonychia pustulata* when cultivated separately and in mixed populations with *Paramecium caudatum* and *Paramecium aurelia*. *Stylonychia* is eventually displaced when living in competition with either *P. caudatum* or *P. aurelia*.

(Redrawn from G. F. Gause, *op. cit.*, reprinted by permission.)

experiments, which were made with peas but disclosed principles that have been found universally applicable. An important feature of the work is that it is capable of mathematical expression. Experimental studies of this sort and ecological studies of the larger forms of plant and animal life have thus demonstrated the reality of the struggle for existence and made a beginning of its precise analysis.

With heritable variations and their basis in the germ cells so much better understood than in Darwin's time, it becomes possible to study the development of gene complexes, as conditioned by environment, and so the occurrence in the individual of the characters presented for selection. With the struggle for existence verified by experimentation, it becomes possible to examine in a more critical manner the effects

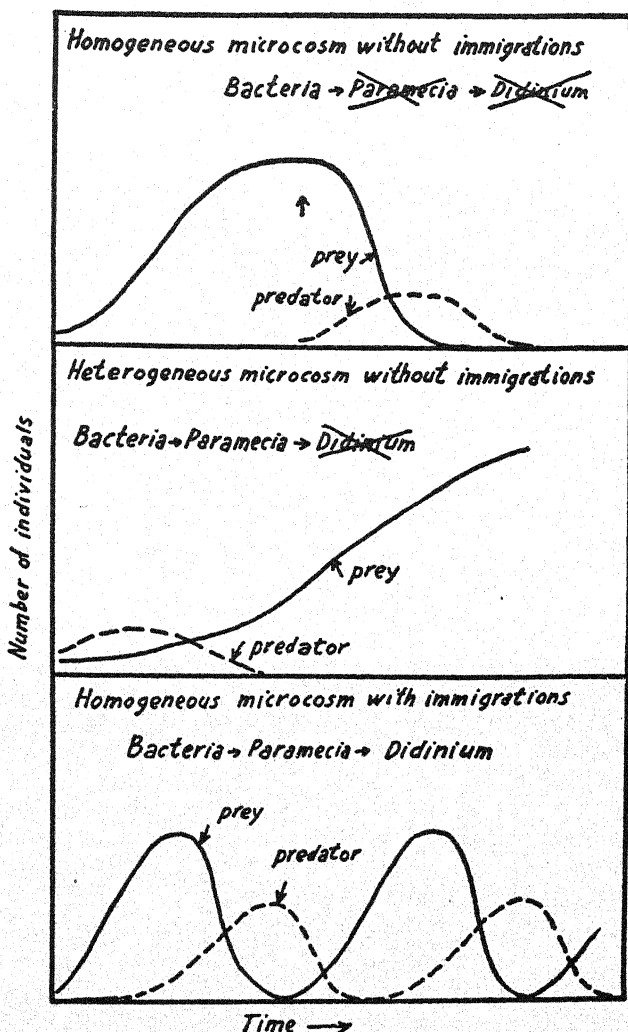


FIG. 517. Schematic representation of the prey-predator relationship between *Paramecium* and *Didinium* when isolated in a culture with bacteria. In a homogeneous culture, both the prey, *Paramecium*, and the predator, *Didinium*, die out. In a heterogeneous culture, which includes a "refuge" of sediment for the *Paramecium*, the prey survives the predator. In a homogeneous culture with periodical introductions of the predator, as might occur in nature, the prey and predator populations rise and fall rhythmically.

(From G. F. Gause, *op. cit.*, reprinted by permission.)

of the struggle upon heritable variations. The mathematics of chance has proved an effective tool in these studies, the nature of which cannot be presented within a brief compass. How and when natural selection begins to work is not precisely determined, but the concept of

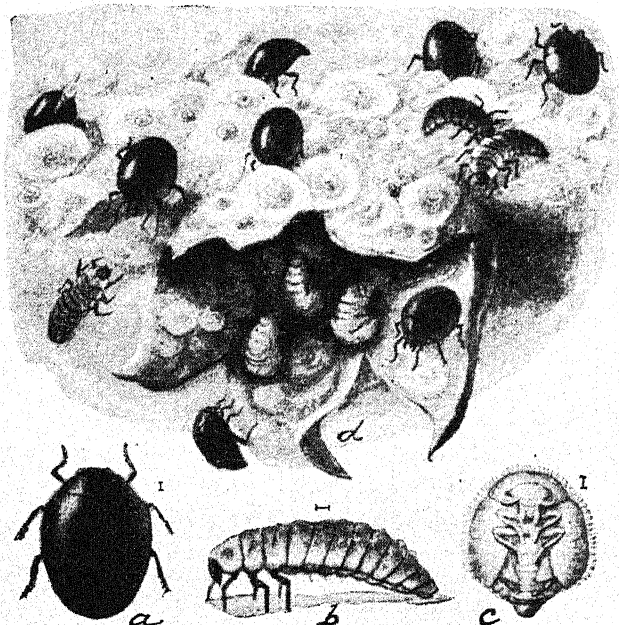


FIG. 518. The ladybug, *Pentilia misella*, and its larvæ, feeding upon another insect, the San José scale, a dangerous enemy of fruit trees. Various species of the ladybugs, which are members of the Coleoptera, have proved to be efficient checks upon the multiplication of scale insects. *a*, adult; *b*, larva; *c*, pupa; *d*, adults and larvæ feeding upon the scale insects, the scalelike bodies of which are shown upon a twig of a pear tree.

(From L. O. Howard and C. L. Marlatt, Bulletin 3, N. S., U. S. Dept. Agriculture, Division of Entomology.)

selection is apparently sustained as a factor whereby the course of evolution has been directed along the lines of adaptive modification in the general manner that Darwin supposed. The extent to which any character is actually adaptive, and thus the product of selection, must be examined no less critically than other problems. Although the Theory of Natural Selection now rests upon a stronger although more restricted foundation, Darwin's subsidiary theory of *Sexual Selection*, by which the most attractive or vigorous males of certain species were supposedly selected for mating by the females, has not met the test of

critical examination so successfully. In like manner, the alleged phenomena of *mimicry*, of *warning*, and of *signal coloration*, which were supposedly explicable by natural selection, are now questioned as to their reality, to say nothing of their explanation by selection.

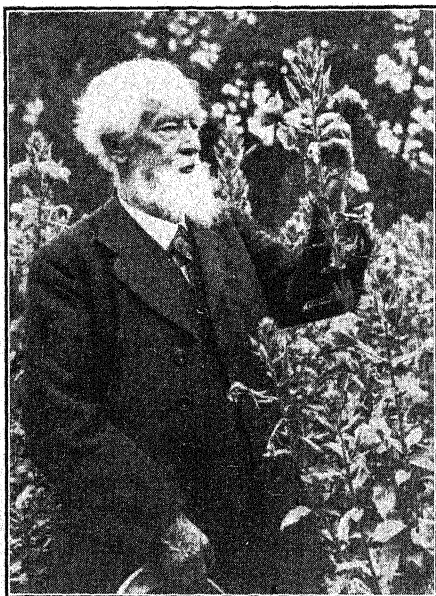
The Mutation Theory of de Vries

Historical. The work of the Dutch botanist, Hugo de Vries (1848–1935), is representative of the more critical study of evolutionary problems that developed toward the end of the nineteenth century. In addition to being one of the independent rediscoverers of the Mendelian principles, de Vries (Fig. 519) became the author of the so-called Mutation Theory, which marked an important step toward the present understanding of heredity and variation.

Nature and Status of de Vries' Theory. In a population of the evening primrose, *Oenothera lamarckiana*, which was growing wild near Amsterdam, Holland, de Vries found several aberrant types along with the typical form. When the typical form was self-fertilized and the seeds were planted, these new types reappeared in small numbers year after year and generation after generation. Moreover, the new types bred true, except that they gave occasional aberrant types, as did the parent type. This fact led de Vries to believe that new types, comparable in some instances with the varieties or subspecies of plants and animals that are frequently recognizable in nature, were appearing in the evening primrose and that he was actually observing initial steps in evolution. The new characters appeared all at once in an individual and were inherited as such by its offspring. It remained to be shown that these *mutations*, as de Vries called them, were sufficiently common to furnish the material for evolutionary changes. He believed this to be the situation in *O. lamarckiana* and at certain times in the history of any race. Natural selection was not eliminated, according to de Vries, since useful mutations were even more likely to survive in nature than the lesser variations which Darwin thought were most important for selection. De Vries' experiments demonstrated what kinds of variations were inherited and so what kinds could be effective in evolution, if selected.

The theory was also suggestive in connection with the breeding of domestic plants, since the extreme variations known to Darwin as *saltations* or *mutations* and as the "sports" recognized by breeders appeared to be phenomena comparable with these changes of *Oenothera*. Certain domestic breeds seem to have originated from such "mutations" which arose fully formed and the descendants of which were se-

lected with considerable inbreeding until the type became established. The Ancon sheep, a short-legged breed descended from a single ram which appeared in 1791, the hornless or polled Hereford cattle descended from a single calf born at Atchison, Kansas, in 1889, tailless cats and dogs, and hairless cats, dogs, mice, and horses are further examples of



Hugo de Vries.

FIG. 519. Hugo de Vries (1848-1935) and his *cennotheras*.

(From R. E. Cleland, 1935, *Journal of Heredity*, vol. 26, reprinted by permission.)

conspicuous variations arising in a fully developed state and sometimes capable of perpetuation (Fig. 524).

The current use of the term mutation has been explained in Chapter 6. The Mutation Theory of de Vries seemed of great importance when it was proposed, and it served to advance the science of genetics. At the present time its importance is largely historical, because the conspicuous changes which de Vries termed mutations do not seem to be the mutations that have been most important in evolution. It even seems probable that most of the so-called mutations he observed in *Cenothera* are really complex and rather stable hybrid combinations and not mutations at all in the sense that this term is now used by geneticists.

Other Theories Concerning Evolution

Isolation. Since free interbreeding tends to promote uniformity in a population, some degree of isolation is necessary for the individuals

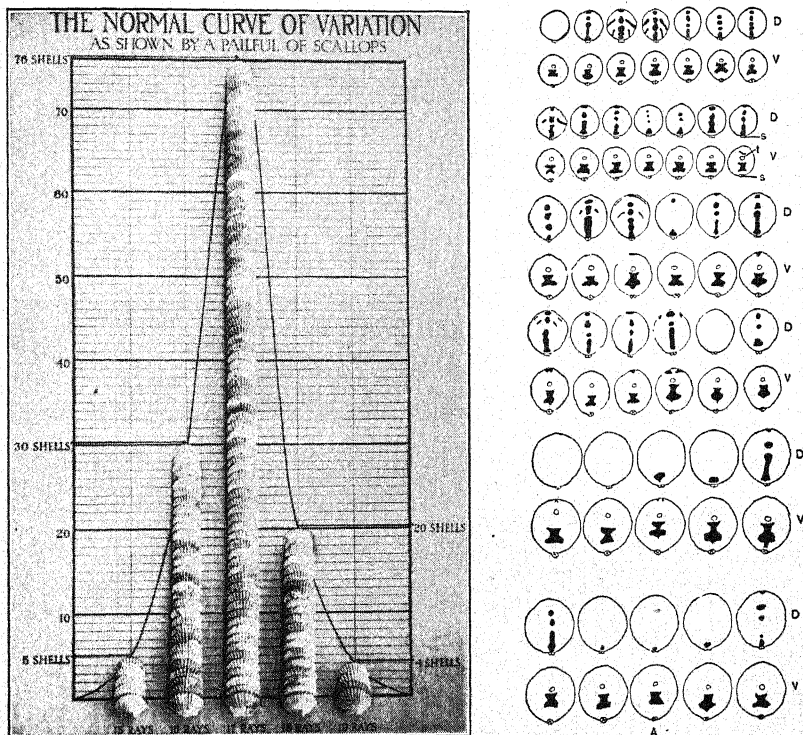


FIG. 520. Fluctuations: *Left*, variation in the number of rays on the shells in a pail of scallops, *Pecten irradians* (cf. Fig. 312, p. 427). Individuals of any species selected at random and measured for any feature usually show a curve of variation of this general type, although a study of the descendants of single individuals may resolve the group into a number of pure lines, each with its curve of fluctuating variations (cf. Fig. 102, p. 164, and Fig. 521). *Right*, variation in the size and pattern of the color markings on dorsal (D) and ventral (V) sides of abdomen of the black-widow spider, *Latrodectus mactans*.

(*Left*, photograph by courtesy of American Museum of Natural History. *Right*, from A. M. Reese, 1940, *Journal of Heredity*, vol. 31, reprinted by permission.)

possessing variations that become steps in evolutionary change. From the standpoint of genetics the conditions in nature that effect such isolation can be grouped as shown by the tabulation designated Figure 523. A classic example of the ecological isolation noted in this tabula-

tion is the distribution of snails of the Family *Achatinellidæ*, as they were found in the Hawaiian Islands during the fifties of the nineteenth century by John T. Gulick (1832-1923). Snails of this family (Fig.

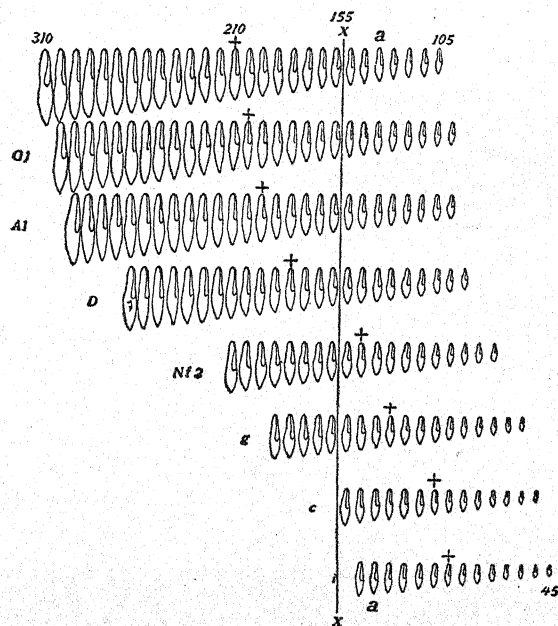


FIG. 521. Fluctuations in pure lines of *Paramecium*. By rearing pure lines, or the descendants of single individuals of *Paramecium*, it is found that each pure line fluctuates between certain limits. If all the individuals of this figure were plotted in a single curve, the result would be a curve of variation similar to that shown in Fig. 520 (cf. Fig. 102, p. 164). In the present figure, each row represents a single pure line, showing the maximum, minimum, and intermediate sizes of the individuals. The differences in size within the pure line are fluctuations due to differences in growth and environment. The differences in average size between the several lines are hereditary. The numbers show the length in micra. The average length for all the lines taken together is given by the perpendicular line $x-x$ at 155 micra. The average size for each pure line is that of the individual above which is placed a + sign. Other letters represent the investigator's special designations.

(From H. S. Jennings, 1909, *American Naturalist*, vol. 43.)

522) live upon trees. Since they cannot travel any distance over a land surface devoid of shade or moisture, their distribution is restricted. On the island of Oahu there are, along the sides of the principal mountains, small valleys in which these snails find suitable habitations, but they

cannot easily cross the ridges between neighboring valleys nor the crest of the mountain. Neither can they move out upon the plain below. A population that became established in any valley would tend to remain isolated as long as similar climatic and topographical conditions prevailed. At the time of his original collecting, Gulick found that almost every small valley had its particular species or subspecies, differing in size, color, and shape of the shell. Some of the more recent collectors even report a species that seems to have been restricted to a single tree which was sufficiently isolated to prevent migration. Differences of the sort indicated can hardly be explained by natural selection, since this would postulate greater differences in the environments, that is, as many standards of selection as the types evolved. The environment in all the valleys is essentially the same. Moreover, the differences between the species can hardly be regarded as useful and thus having a selective value under the observed environments. The most reasonable explanation of the facts seems to be that, when populations are thus isolated, each tends to change into a particular type, because of the somewhat different individuals originally present or subsequently appearing in each population. In the language of genetics each population would be made up originally of individuals with certain combinations of genes, no two populations being identical. The mere sequence of generations would produce different combinations in each locality, and mutations would also occur. From these possibilities, in accordance with the laws of chance, would be brought forth different types and hence evolutionary changes.

Other examples of the same sort have been studied, notably the marine Genus *Thais* in the vicinity of Friday Harbor, Washington, and the Genus *Partula* in Tahiti. The snails belonging to *Thais* live on rocky shores and will not cross sand or go into deep water. Since their young are hatched as miniature adults, there is no dispersal as free-swimming larvæ. Each rocky point or other area that is isolated from other suitable regions has its particular species or subspecies. The Genus *Partula* presents the same kind of picture. There is also evidence that important changes in the distribution and characteristics of some of the species of *Partula* have occurred since they were first studied in 1860-1863.

Mechanisms of isolation involving the reproductive functions, gametes, and zygotes (Fig. 523) are probably of more importance in evolution than ecological isolation. They have been observed in many instances and tested experimentally. It appears that the isolation thus effected in nature is definitely related, on the one hand, to the establishment of subspecies or lesser groups that breed among themselves

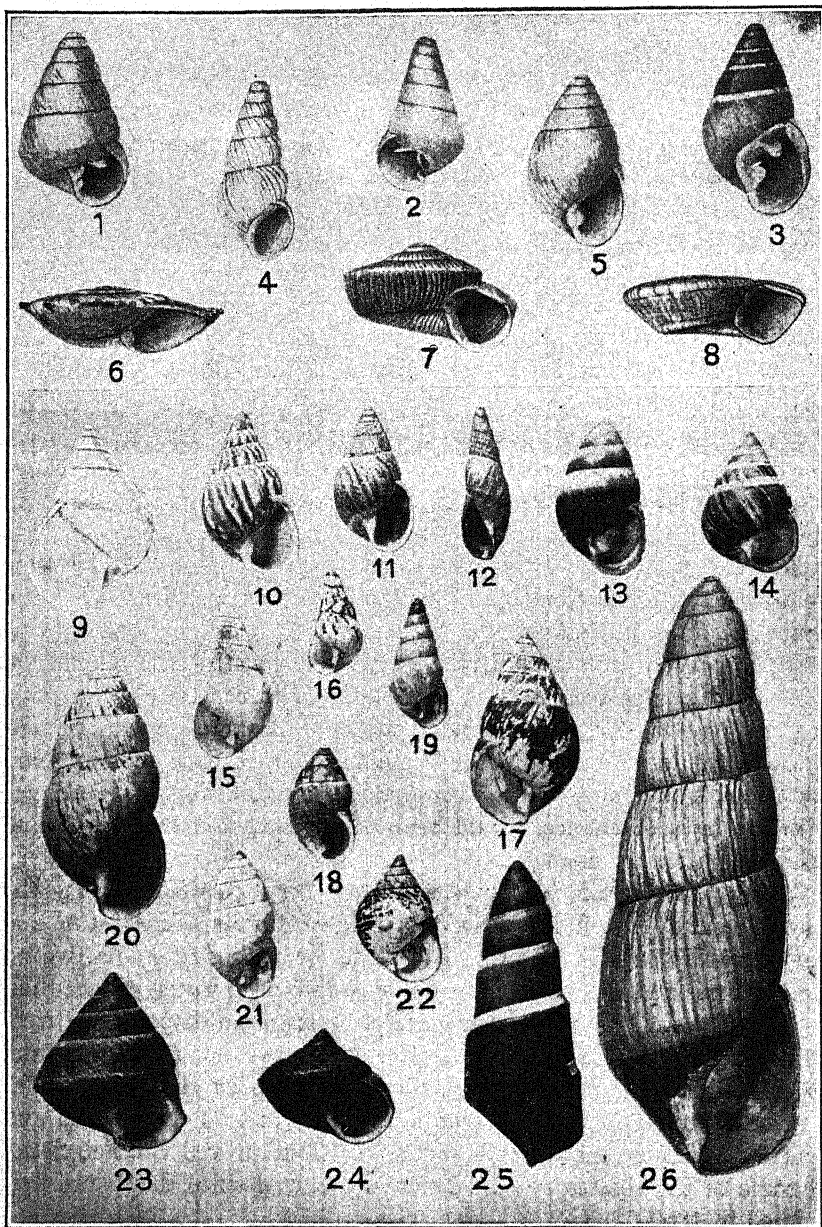


FIG. 522. The land snails shown on this plate are found only on the Hawaiian Islands, which are oceanic islands and have never been connected with a mainland. The most probable explanation of the origin of such a land-snail population is that minute ancestral forms were carried to the islands by hurricanes; from the limited numbers of such arrivals it is supposed that the existing population with more than 600 species has been evolved.

(From A. Gulick, "John Thomas Gulick," copyright, 1932, by University of Chicago Press, reprinted by permission.)

and, on the other, to a selective process that may subsequently occur. If one mechanism is insufficient, the total effect of several such mechanisms may be the virtual isolation of one group from another in their breeding. Thus, interbreeding between two races, *A* and *B*, of *Drosophila pseudoöbscura* is impeded by a pronounced, although incomplete, geographical isolation, by marked sexual isolation, by complete sterility of the F_1 hybrid males and part of the back-cross males, and by a low viability of certain other crosses. Although no one of these isolating factors might be sufficient in itself, they seem effective as they exist collectively in nature. A few individuals of a new type may thus be kept from mating with the parent stock and so from disappearing, until their numbers increase to a significant fraction of the population. Species in nature seem to consist of such lesser types, races, subspecies, or varieties as they are variously called. Although it appears that these races may come into existence independently of natural selection, it also appears that, once established, such a race may be selected in competition with other races if it has a higher survival value. The appearance of heritable variations in a few individuals, establishment by isolation of a race possessing these characteristics and its resultant increase in numbers, and the eventual possibility of its selection as a race seem to be steps that occur in evolution. The scope of natural selection is limited in a sequence of this sort; but, on the other hand, natural selection is relieved of the incipient stages which have often been cited as difficult to explain in terms of the earlier picture of the selective process. If isolation thus assumes the most important rôle at one stage of the process, it must be regarded as a very significant factor.

At the present time these problems of isolation are the subject of many investigations by geneticists, ecologists, and taxonomists. The origin of *incipient species*, as they may be called, is recognized as the next step in evolution after the heritable variations have appeared. Current investigations involve the technical data of variation and heredity to such an extent that they cannot be described without extended explanations of the genetic principles involved. However, it is possible, without this knowledge of genetics, to understand that the appearance of heritable variations and their perpetuation first in small groups of individuals and then in larger groups which eventually become species are the first steps in evolution. Thus, one species may arise from a pre-existing species and a third species from the second; and so, great evolutionary changes may occur in the course of time. Darwin called his book "The origin of species" because the origin of species is the clue to the evolutionary process.

I. Mechanisms that prevent the production of the hybrid zygotes or engender such disturbances in the development that no hybrids reach the reproductive stage. "Incompatibility of the parental forms" may be used as a general term for such mechanisms.

A. The parental forms do not meet.

- a. *Ecological isolation.* The potential parents are confined to different habitats (ecological stations) in the same general region and therefore seldom or never come together, at least during the reproductive age or season.
- b. *Seasonal or temporal isolation.* The representatives of two or more species reach the adult stage at different seasons, or the breeding periods fall at different times of the year.

B. The parental forms occur together, but hybridization is excluded, or the development of the hybrids is arrested.

- a. *Sexual or psychological isolation.* Copulation does not occur because of the lack of mutual attraction between the individuals of different species. This lack of attraction may in turn be due to differences in scents, courtship behavior, sexual-recognition signs, and the like.
- b. *Mechanical isolation.* Copulation or crossing is difficult or impossible on account of the physical incompatibilities of the reproductive organs.
- c. *The spermatozoa fail* to reach the eggs or penetrate into them; in higher plants the pollen-tube growth may be arrested if foreign pollen is placed on the stigma of the flower.
- d. *Inviability of the hybrids.* Fertilization takes place, but the hybrid zygote dies at some stage of development before it becomes a sexually mature organism.

II. Hybrid sterility prevents the reproduction of hybrids that have reached the developmental stage at which the parents normally breed. Sterile hybrids produce either no functional gametes or gametes that give rise to inviable zygotes.

FIG. 523. Mechanisms effecting isolation.

(Based upon table in Dobzhansky, "Genetics and the origin of species," 1941, Columbia University Press.)

Hybridization. The crossing of distinct species has been proposed as a source of new species in nature, irrespective of any selection of the new combinations that might thus be formed. The Dutch botanist, J. P. Lotsy (1867-1931), collected a considerable amount of evidence for such hybridization as a factor in evolution. The diffi-

culties with this proposal are that hybridization appears to be uncommon in nature and that species do not differ in the manner that might be expected if they had been formed to any great extent by this means. It does seem true that hybridization between strains within domestic species has sometimes produced new types that have given rise to new varieties under artificial selection, particularly in plants.

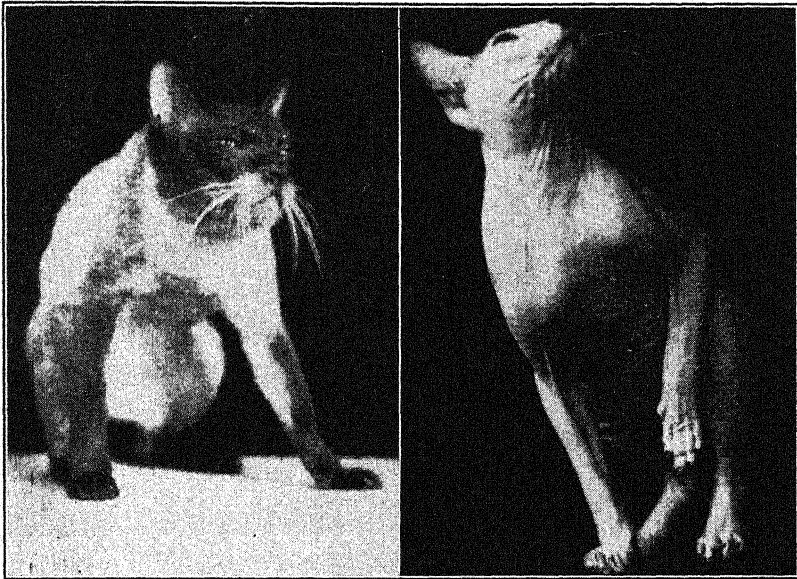


FIG. 524. Normally haired cat and hairless mutant of same stock.

(From E. Letard, 1938, *Journal of Heredity*, vol. 29.)

Orthogenesis. This term has been variously used to indicate a "straight" genesis or evolution directed by Lamarckian factors or by natural selection or, more properly, to indicate an evolution directed by internal factors. True, in some cases evolution seems to have proceeded along a certain course, for example, the increasing size of such forms as the horses, elephants, and dinosaurs; the reduction of digits in the horse series; and, in the extinct mammals called titanotheres, the formation of horns, which first appeared as protuberances that were hardly distinguishable and presumably not useful but increased as though destined to follow a certain course. Again, many fossil series suggest that types begin simply and evolve complexities, such as overgrown spines and plates, and that such overdevelopment precedes extinction. A few isolated examples would not be significant, but some zoölogists and a larger number of paleontologists claim that evolution of this

general sort has occurred so often in widely different types of animals that it can be explained only as a result of fundamental forces inherent in a race and carrying it along a straight or orthogenetic course. The fact that mutations do not appear at random and that the same mutation may occur repeatedly is cited by advocates of this theory as evidence from existing plants and animals. There has thus arisen the concept of a "perfecting principle," or "inner cause," or "law of progress," that has directed the evolution along the paths in question. The distinction should be made between the seemingly orthogenetic course observed and the postulation of an internal orthogenetic factor to explain such an observed course.

Throughout the preceding discussion the origin of heritable variations has been emphasized as the basic factor to be explained in any comprehensive theory of evolutionary change. The Lamarckian Theory supposes such variations to result from use and disuse and from the direct effects of the environment upon somatic cells. The Darwinian Theory assumes the appearance of heritable variations, which are selected, without attempting to explain their origin. Heritable variations, as distinct from fluctuations, are the variations involved according to the data of genetics, whatever their manner of origin. The concept of an internal orthogenetic factor postulates the origin of heritable variations along a directed line and hence a directed course of evolution. This internal factor might be considered an outcome of physico-chemical sequences and hence mechanistic, but it seems most commonly to have been regarded in a vitalistic and mystical sense. For this reason and because there seem no means for experimental proof of orthogenesis the concept has not been highly regarded by many biologists.

Emergent Evolution. What is called emergent evolution has been proposed as an important factor in the history of organisms. The concept of emergence is often illustrated by the formation of a chemical compound. Hydrogen and oxygen possess certain properties which do not resemble the familiar properties of water. Certainly with our existing knowledge anyone who had never seen water could not predict its properties from those of hydrogen and oxygen. When hydrogen and oxygen combine, it can be said that something new is formed, or "emerges," namely, water. At the other end of the scale, it could be said that human intelligence emerged in the course of evolution, in the sense that such intelligence represents something new resulting from a combination of parts never before united. Explanations of this nature seem verbal rather than scientific and do not appeal to the majority of biologists. Many riddles of evolution are inexplicable on

the basis of present knowledge. Doubtless some of them never will be explained. To say that the whole is greater than its parts and that something new emerges in the manner indicated is unsatisfactory as a scientific explanation.

Evolution of Useless Characters

Useless characters, along with those that are useful, seem to be common in organisms. This is particularly true for the structural features of animals; it is more difficult to decide that any functional character is useless. Although the appearance of variations apparently useless to their possessor is frequently observed in genetic studies, the survival and further evolution of such variations are not easy to explain. The theory of natural selection, by its very nature, can offer no explanation, and none of the other factors enumerated is suggestive, unless it be orthogenesis. To say that the characters evolved in organisms must be, for the most part, useful to their possessors and that a certain percentage of useless or not too harmful characters are carried along with a majority of useful ones does not explain the matter, although it may give the clue to an explanation. The problem remains unsolved. Progress toward its solution may disclose factors in evolutionary change that have not yet been recognized.

Summary

The history of organisms, as indicated by the data of biological and other sciences, has been a process of gradual change from some primitive form or forms of life. How and where these primitive forms originated on our planet is a matter of speculation. There are suggestions that the place of origin was the primitive oceans. The time of origin must have been a period after these waters had cooled sufficiently to permit life. Evidence for the evolutionary changes that have produced existing forms from this primitive ancestry is drawn from a wide range of observations and experiments. The facts of distribution, both geologic and geographic, and the facts of anatomy, embryology, and physiology can be reasonably explained in accordance with the doctrine of evolution. The strength of this circumstantial evidence is its extent and diversity. Any other explanation of the data is a violation of common sense as well as scientific reasoning. Experimental evidence, derived from the practices of animal breeding and from technical study of the problem, confirms the conclusion based upon the circumstantial evidence that the only reasonable explanation for a vast

array of facts is evolution. Mankind is not exempt, since the evidence points clearly to the origin of man as an offshoot from the mammalian stock that produced the higher apes and so from a remote ancestry in common with other vertebrates.

With the historic fact of evolution and something of its course thus established, there remain the factors that have conditioned such changes. They have not been fully established, but it is evident that variation and heredity are the beginning of evolutionary modifications, that isolation of incipient stages is important, and that natural selection has directed evolution along lines useful to the organisms concerned. These have certainly been among the factors conditioning evolution. The case has not been established for the Lamarckian doctrine. The doctrines of orthogenesis and of emergent evolution do not appeal to many biologists. The evolution of useless characters, which seems to have occurred, remains a problem.

Manifestly, only the cell doctrine can rank with the doctrine of evolution as a generalization of biological science. Development of the cell doctrine has been related to great advances in the understanding and in the practical applications of biological science. Development of the evolutionary doctrine has been no less important because it has necessitated adjustment in many fields of thought. Much of this adjustment is still in progress.

GLOSSARY

This glossary is not a complete dictionary of zoölogical terms nor even of all such terms used in this book. Words that are used in a limited part of the book are defined where they occur, and the student is referred to the Index in such cases.

A-. Combining form, meaning "without."

ABDOMEN. That part of the trunk of a vertebrate which is posterior to the thorax and separated from it by the diaphragm, and which contains that part of the cœlom known as the abdominal or peritoneal cavity. In the arthropods, the posterior division of the body.

ABORAL. Opposite the mouth.

ABSORPTION. The taking in of soluble foods by the circulating fluids.

ACQUIRED CHARACTER. A phrase used as a synonym for somatic variation or fluctuation in Lamarck's Theory of the Inheritance of Acquired Characters. Since all the characters of any individual are acquired as the zygote develops, the phrase is an unfortunate one.

ACTIVATION. The initiation of development, usually the result of the union of an egg and a sperm. *Cf.* PARTHENOGENESIS.

ADAPTATION. Any modification of an organism that better fits it for existence in its present environment or enables it to live in a different environment.

ADDUCTOR MUSCLE. A muscle that draws a part toward a central region or median line.

ADSORPTION. The accumulation of particles on a surface.

AFFERENT. Carrying to or toward a given region. *Cf.* EFFERENT.

AGAMETE. Any single cell, other than a gamete, that can reproduce the organism.

AIR-TUBES. Tubes conveying air to the lungs in vertebrates and from the spiracles to the cells in certain arthropods.

ALBUMEN. The white of the reptile's and bird's egg, surrounding the yolk, or zygote, and used as food by the embryo.

ALGÆ (*sing.* ALGA). A group of green plants with relatively simple organization.

ALLELOMORPHS. Genes located in comparable positions on homologous gene-strings but producing alternative effects in a given character; for example, gene *A* might condition the appearance of black hair, while an allelomorph, gene *a*, might condition the appearance of white hair.

ALTERNATION OF GENERATIONS. *See* METAGENESIS.

ALVEOLUS (*pl.* ALVEOLI). A small cavity, such as any one of the minute air-sacs in the mammalian lung or a secreting portion of an alveolar gland.

AMBULACRAL. Pertaining to the rows of openings through which the tube feet of enchinoderms are extended; hence, ambulacral system of which the tube feet are a part.

AMINO ACIDS. Organic acids containing an amino group (NH_2); proteins are made up of amino acids.

AMITOSIS. Direct nuclear division, without the formation of chromosomes. *Cf.*

MITOSIS.

- AMOEBOID. Pertaining to or resembling an amoeba; usually used with respect to locomotion.
- AMPHIBIOUS. Living both on land and in water.
- AMPHIMIXIS. The fusion of the nuclei of the two gametes that give rise to a zygote.
- AMPULLA (*pl.* AMPULLÆ). A flask-shaped structure.
- ANABOLISM. *See* ASSIMILATION.
- ANÆROBIC. Able to live in the absence of free oxygen, that is, by anærobic respiration in contrast to the common form of respiration, which is aerobic.
- ANALOGY (*adj.* ANALOGOUS). Correspondence in function. *Cf.* HOMOLOGY.
- ANATOMY. The science of the structure of animals as revealed by dissection; gross morphology. *Cf.* HISTOLOGY.
- ANIMAL HEMISPHERE. That half of a telolecithal egg in which the nucleus is located and which contains less yolk than the vegetal hemisphere.
- ANIMAL POLE. That point on the surface of an egg at which the polar bodies are formed; one end of the egg-axis. *Cf.* VEGETAL POLE.
- ANISOGAMETES. Gametes of unequal size that unite in pairs. *Cf.* ISOGAMETES.
- ANISOGAMY. Fusion of gametes of unequal size. *Cf.* ISOGAMY and FERTILIZATION.
- ANTERIOR. Pertaining to or situated toward the head; the end which is directed forward during locomotion; the end which contains the mouth. *Cf.* POSTERIOR.
- ANTHROPOLOGIST. One who studies the science of mankind.
- ANUS. The posterior opening of the digestive tract.
- APPENDAGE. Any limb or peripheral part of the body that diverges from the principal axis; specifically, the limbs of arthropods and vertebrates.
- AQUATIC. Pertaining to water; living in water.
- ARCHENTERON. The gastrula cavity.
- ARREST. Suspension of a movement or process.
- ARTERY. A blood vessel carrying blood from the heart to capillaries. *Cf.* VEIN.
- ARTHO-. Combining form, meaning "joint."
- ARTIFACT. A natural object modified by man, such as a stone implement.
- ARTIFICIAL PARTHENOGENESIS. *See* PARTHENOGENESIS.
- ASEXUAL. Not sexual or not produced by sexual processes.
- ASEXUAL REPRODUCTION. Reproduction without formation and union of gametes. *Cf.* SEXUAL REPRODUCTION.
- ASSIMILATION. The building up of the constituents of protoplasm from suitable materials brought to the cell; the synthesis of protoplasm. *Cf.* DISSIMILATION.
- ASYMMETRY. Absence of symmetry.
- ATRIUM (*pl.* ATRIA). A membranous sac which serves as a passageway, such as the atrium (auricle) of the heart and the genital atrium.
- AUDITORY. Pertaining to hearing or to the organs related to hearing.
- AURICLE. The external ear of mammals or something that resembles such a projection; more specifically, a thin-walled, laterally expanded part of the heart that receives blood from the veins.
- AUTOSOME. Any chromosome other than the sex chromosomes.
- AUTOSOMES. Chromosomes that occur in pairs of similar size and shape and in equal numbers in both males and females of a species; chromosomes other than the sex chromosomes. *Cf.* SEX CHROMOSOMES.
- AXIAL. Pertaining to the central line, or axis, of any symmetrical body; for example, the axial skeleton of vertebrates is composed of the skull and vertebral column.

BACKBONE. The vertebral column.

BACK-CROSS. A cross between a hybrid of the F_1 or F_2 generations and either of the parent types; a back-cross with the recessive parent type is used to distinguish heterozygous and homozygous individuals showing the dominant characteristics in an F_2 generation.

BACTERIA (*sing.* BACTERIUM). Microscopic, unicellular, colorless plants.

BARRIER. Any obstruction that prevents migration.

BEHAVIOR. The total reactions of an organism to its external environment.

BI-. Combining form, meaning "two"; same as DI-.

BILATERAL SYMMETRY. The symmetry of right and left halves of the body.

BIOGENESIS. The production of living things from living things, not from non-living things; opposed to abiogenesis, or spontaneous generation; includes both reproduction and organic evolution.

BIOLOGY. The science of living things, both plants and animals; derived from *bios*, meaning life.

BIRADIAL SYMMETRY. A bilateral symmetry obviously derived from radial symmetry.

BLASTODERM. The developing part of the egg of a fish, reptile, or bird in which partial cleavage occurs; it gives rise to both the embryo and the embryonic membranes.

BLASTODISK. That part of the egg of a fish, reptile, or bird in which the nucleus is located and in which cleavage will occur.

BLASTOPORE. The opening of the gastrula cavity (archenteron) which is surrounded by the lips of the blastopore, or the germ ring.

BLASTULA. A developing individual characterized by a monoblastic structure.

BLASTULA CAVITY. The cavity of the blastula; cleavage cavity, or blastocoel.

BODY CAVITY. Any extensive cavity or series of cavities within the mesoderm. *See* COELOM and PSEUDOCOEL.

BODY-PLAN. The fundamental plan of organization of layers, cavities, and organ-systems in animals.

BRANCHIAL. Pertaining to branchiæ, or gills.

BRANCHIATE. Having gills as organs of external respiration. *Cf.* PULMONATE.

BROOD-POUCH. Any cavity, other than a part of the reproductive tract, in which eggs or young are received and retained during at least a part of the developmental period.

BUCCAL. Pertaining to the mouth.

BUDDING. A method of reproduction by unequal cell division, as in unicellular organisms, or by repeated divisions of totipotent cells to form an outgrowth, as in the coelenterates.

CÆCUM (*pl.* CÆCA). A blind pouch attached to any part of a digestive tract.

CALCAREOUS. Containing lime; chalky.

CAPILLARY. One of the many minute, thin-walled blood vessels found in organs of the body; substances enter and leave the blood through the walls of such vessels.

CARDIAC. Pertaining to or situated near the heart.

CARNIVOROUS. Feeding upon animals. *Cf.* HERBIVOROUS and OMNIVOROUS.

CASTE. Any one of the distinct forms of one species found among the social insects, such as the termites.

CATABOLISM. *See* DISSIMILATION.

- CAUDAL.** Pertaining to or situated toward the tail.
- CAUSE.** The set of conditions as a result of which something occurs; frequently used for what is considered to be the most important of these conditions.
- CELL.** A mass of protoplasm containing one or more nuclei at some stage in its differentiation; the unit of structure and function in animals and plants.
- CELL DIFFERENTIATION.** The formation of tissue cells and gametes during histogenesis and gametogenesis, respectively; characterized by changes in the cytosome, or in the nucleus, or in both.
- CELL DIVISION.** The method of origin of new cells from pre-existing ones.
- CELL LOCALIZATION.** The bringing of groups of cells into definite positional relationships with other cell groups; brought about by cell movements.
- CELL PRODUCTS.** Non-cellular materials built up within cells and passing out of cells.
- CELL SPECIALIZATION.** The formation of different kinds of somatic cells associated with a physiological division of labor during the evolution of organisms; sometimes used to mean cell differentiation.
- CELLULAR.** Consisting of or pertaining to cells.
- CENTIMETER.** The hundredth part of a meter; one inch equals 2.54 centimeters.
- CEPHALIC.** Pertaining to or situated toward the head.
- CEPHALIZATION.** The localization of important parts, such as the sense organs and the central nervous system, toward or in the head region during the evolution of organisms.
- CEPHALOTHORAX.** A body division formed by the fusion of the head and the thorax in some of the arthropods.
- CHEMICAL COÖRDINATION.** Coördination brought about by the reaction of parts to the stimuli produced by endocrines that circulate in the blood. *Cf.* COÖRDINATION and NERVOUS COÖRDINATION.
- CHEMORECEPTOR.** A receptor sensitive to chemical substances in solution.
- CHITIN.** The chemical substance characteristic of the exoskeletons of arthropods.
- CHLORAGOGUE LAYER.** The outer layer of the stomach-intestine of the earthworm and some other annelids.
- CHLOROPHYL.** The green coloring matter of plants.
- CHROMATID.** A half-chromosome; one of the four half-chromosomes forming a tetrad.
- CHROMATIN.** The readily stainable substance of the nucleus, most conspicuous during mitosis.
- CHROMATOPHORES.** Pigment-bearing cells, frequently capable of changes in shape and responsible for the color changes in animals like the chameleon and the squid.
- CHROMONEMATA** (*sing.* CHROMONEMA). Slender threads of chromatin which can be distinguished within the chromosomes during mitosis and, in some cases, in the nucleus between periods of division.
- CHROMOSOMAL ABERRATION.** Any loss or gain of a part of a particular chromosome, of a whole chromosome, or of a haploid set of chromosomes; may give rise to a heritable variation.
- CHROMOSOME.** A mass of chromatin, of characteristic size and shape, visible in the nucleus at the time of mitosis; composed of a matrix containing at least two chromonemata.
- CILIA** (*sing.* CILIUM). Short, hairlike extensions from the free surfaces of certain cells; capable of vibration and usually numerous. *Cf.* FLAGELLUM.

CIRCULATING FLUIDS. Blood and lymph.

CIRRUS (*pl.* CIRRI). A slender extension, occurring singly or in groups and frequently curved; a name used for many structures of diverse functions.

CLASS. One of the subdivisions of a phylum; a group of next higher rank than an order.

CLASSIFICATION. The grouping together of those organisms which have certain structural features in common.

CLEAVAGE. Cell division during the early period of development.

CLEAVAGE CAVITY. *See* BLASTULA CAVITY.

CLOACA. A common chamber through which egested and certain excreted materials, as well as the germ cells, leave the bodies of many vertebrates; analogous regions in some invertebrates.

CM. Abbreviation for centimeter.

COELOM. A body cavity having, typically, a peritoneal lining and a characteristic relation to reproductive organs and nephridia; the "true coelom." *Cf.* BODY CAVITY, SCHIZOCCEL, and HEMOCCEL.

COELOM (*pl.* COELOMATA). The so-called body cavity of triploblastic Metazoa, formed in and surrounded by the mesoderm; may be continuous or divided into chambers by partitions.

COLLOIDAL SYSTEM. A type of physical organization in which particles of a certain size range are dispersed in a solution.

COLONY. A group of individuals, unicellular or multicellular and of the same species, which have arisen from a common parent cell and remain attached or held together; also used of insect societies.

COMMENSALISM. An association of two or more individuals, of different species, in which none is parasitic and in which some benefit may result to one or more. *Cf.* PARASITISM and SYMBIOSIS.

COMMISSURE. A connection between two ganglia of a pair, or right and left parts of the nervous system. *Cf.* CONNECTIVE.

COMMON CARRIER. A circulating fluid which transports numerous substances to and from the various parts of the body.

COMMON CENTER OF ORIGIN. A place in which the ancestors of different but related kinds of animals lived and from which they migrated over all possible routes as evolution occurred.

CONDITION. To be a prerequisite of some event.

CONDITIONED REFLEX. A reflex action in which the stimulus is not a natural one but has been established by training or experimentation.

CONJUGATION. Temporary union of two cells during which exchange of nuclear materials occurs, as in *Paramecium*. *Cf.* FERTILIZATION.

CONNECTIVE. A longitudinal nerve cord extending between ganglia in different regions of the body. *Cf.* COMMISSURE.

CONSTITUENT. That which is a necessary part.

COORDINATION. The working together of different parts of an organism in such a way that it is physiologically balanced. *Cf.* CHEMICAL COORDINATION and NERVOUS COORDINATION.

COPULATION. *See* SEXUAL UNION.

CORTEX (*pl.* CORTICES). An outer or superficial layer.

CRANIAL. Pertaining to the skull.

CROSS-FERTILIZATION. Union of gametes produced by different individuals. *Cf.*

SELF-FERTILIZATION.

CUTICLE. A non-cellular layer secreted by the cells of the outer surface of the body.

CYST. A protective capsule.

CYTOLOGY. The science of the structure of cells.

CYTOPLASM. The protoplasm found in the cytosome.

CYTOPLASMIC INCLUSIONS. Microscopic structures found in the cytoplasm, such as chondriosomes and yolk spheres.

CYTOPYGE. Cell "anus" through which fecal material is egested by some protozoans.

CYTOSOME. The part of the cell surrounding the nucleus and limited by the cell membrane.

CYTOSTOME. Cell "mouth" through which food is ingested by some protozoans.

DATA (*sing.* DATUM). Observed and recorded facts.

DERMAL. Pertaining to the skin or outer covering of the body.

DERMIS. The inner layer of the skin, composed of connective tissue.

DETERMINERS. *See* GENES.

DEVELOPMENT. The transformation of a zygote into an adult multicellular organism; the consecutive processes of cell division, cell localization, and cell differentiation following syngamy.

DI-. Combining form, meaning "two"; same as BI-.

DIAPHRAGM. A partition; specifically, the partition forming the anterior boundary of the peritoneal cavity in mammals.

DIFFERENTIATION. *See* CELL DIFFERENTIATION.

DIFFUSE. To spread, as a fluid; to mix with another substance.

DIGAMETIC SEX. The sex of individuals that produce two classes of gametes which differ with respect to the presence of an X-chromosome; in most animals, the male sex.

DIGESTION. The chemical disintegration of food which precedes its absorption and assimilation.

DIGESTIVE. Pertaining to digestion.

DIOECIOUS. Having sexually differentiated individuals; having the male and female gonads in separate individuals. *Cf.* MONOECIOUS.

DIPLOBLASTIC. Having only two germ layers, the ectoderm and endoderm, and a single cavity which has one external opening and is lined with endoderm. *Cf.* MONOBLASTIC and TRIPLOBLASTIC.

DIPLOID. Having two sets of chromosomes forming homologous pairs, as in somatic cells, primordial germ cells, and zygotes. *Cf.* HAPLOID.

DIRECT CELL DIVISION. *See* AMITOSIS.

DISCHARGE. The passage of a nervous impulse from a nerve fiber to an effector.

DISJUNCTION. The separation of the chromosomes of a homologous pair and their distribution into separate cells during one of the meiotic divisions. *Cf.* SEGREGATION.

DISSIMILATION. The tearing down of the constituents of protoplasm, chiefly by oxidation; the disintegration of protoplasm. *Cf.* ASSIMILATION.

DISTAL. Situated away from the center or place of attachment. *Cf.* PROXIMAL.

DISTRIBUTION. The spreading of organisms over the surface of the earth.

DIURNAL. Pertaining to the daytime. *Cf.* NOCTURNAL.

DOMESTICATION. The taming or rearing of wild animals by man, with the consequent changes in their environments and habits of life.

- DOMINANCE.** The differentiation of a region under the influence of one gene, called the dominant gene, although an allelomorph, called the recessive gene, may be present; where dominance occurs, a heterozygous individual, with a single dominant gene, looks like a homozygous individual with two dominant genes.
- DORSAL.** Pertaining to or situated near the back or upper surface of an animal or part. *Cf.* VENTRAL.
- DUCT.** A tube, or canal, by which a liquid is conducted; usually restricted to such a tube that opens on a surface. *Cf.* VESSEL.
- DUCTLESS GLAND.** *See* ENDOCRINE GLAND.
- DUCTUS** (*pl.* DUCTUS). *See* DUCT.
- ECOLOGY.** The science of the relations of organisms to their external environment.
- ECTODERM.** The outermost of the two germ layers formed during gastrulation; covers the gastrula. *Cf.* ENDODERM and MESODERM.
- ECTOPARASITE.** A parasite that lives on the outside of its host. *Cf.* ENDOPARASITE.
- ECTOPLASM.** The outermost layer of protoplasm in Protozoa.
- EFFECTOR.** A region where a reaction occurs as a result of a stimulus; muscles and glands are effectors.
- EFFERENT.** Carrying away from a given region. *Cf.* AFFERENT.
- EGESTION.** The elimination of indigestible or undigested material from a place of digestion. *Cf.* INGESTION.
- EGG-AXIS.** An imaginary line passing through the center of the egg and the point where the first polar body is formed; connects the animal pole of the egg with the vegetal pole.
- EMBRYO.** A young organism before its hatching or birth and before it is self-sustaining. *Cf.* LARVA and JUVENILE.
- EMBRYOLOGY.** The science of development.
- EMBRYONIC CELL.** *See* TOTIPOTENT CELL.
- EMBRYONIC MEMBRANES.** Cellular membranes formed from the zygote during development and related to the metabolic requirements of the embryo; specifically, the yolk-sac, amnion, chorion, and allantois in vertebrates.
- ENCYST.** To become enclosed in a cyst.
- ENCYSTMENT.** Encasement with a cyst. *Cf.* EXCYSTMENT.
- ENDOCRINE.** A secretion produced by an endocrine or ductless gland and serving as a stimulus in chemical coordination; sometimes called a hormone.
- ENDOCRINE GLAND.** A gland without a duct, the secretion of which passes into the blood stream by diffusion.
- ENDOCRINOLOGY.** The science of the endocrines.
- ENDODERM.** The innermost of the two germ layers formed during gastrulation; surrounds the archenteron; sometimes called entoderm. *Cf.* ECTODERM and MESODERM.
- ENDOPARASITE.** A parasite that lives within its host. *Cf.* ECTOPARASITE.
- ENDOPLASM.** The interior cytoplasm of a protozoan.
- ENDOSKELETON.** An internal skeleton; a cellular supporting structure formed from mesoderm. *Cf.* EXOSKELETON and SKELETON.
- ENERGY.** *See* TRANSFORMATION OF ENERGY.
- ENTEROCOEL.** *See* ENTERON.
- ENTERON.** A digestive cavity lined by endoderm.
- ENTODERM.** *See* ENDODERM.

ENTOMOLOGIST. A student of the insects.

ENVIRONMENT. The total of surrounding conditions, usually with reference to the organism as a whole; in this sense, the external environment, as contrasted with the internal environment, or immediate surroundings of a part of an organism.

ENZYME. An organic catalyst, or substance that affects the rate of a chemical reaction but does not appear as one of its end products; produced by the digestive glands in considerable quantities and apparently by all protoplasm.

EPIDERMIS. The outer cellular layer of the body; the outer layer of the skin.

EQUILIBRIUM. The state of being balanced.

ERYTHROCYTE. A red blood cell. *Cf.* LEUCOCYTE and LYMPHOCYTE.

EUGENICS. The science which applies the principles of genetics for the purpose of human betterment.

EUGLENOID. Pertaining to or resembling the euglena.

EVAGINATION. The movement of a group or layer of cells away from a cavity.
Cf. INVAGINATION.

EVIDENCE. Facts related to some particular event.

EVOLUTION. The process of natural, consecutive change. *Cf.* ORGANIC EVOLUTION.

EXCRETION. The elimination of the waste products of metabolism; any waste product of metabolism.

EXCRETORY. Pertaining to the elimination of metabolic waste products.

EXCRETORY TUBULE. Any small duct which conveys nitrogenous waste products, such as the kidney tubules of vertebrates, the Malpighian tubules of insects, and the nephridia.

EXCURRENT. Affording an exit; leading outward. *Cf.* INCURRENT.

EXCYSTMENT. Emergence from a cyst. *Cf.* ENCYSTMENT.

EXOSKELETON. An external skeleton; a non-cellular structure formed by the superficial ectoderm. *Cf.* ENDOSKELETON and SKELETON.

EXPERIMENTAL BREEDING. Breeding in such a way that the method of inheritance of given characters can be determined. *See* HYBRIDIZATION.

EXPERIMENTAL EMBRYOLOGY. The study of development by altering any one of the conditions affecting its course; such as the external environment.

EXTERNAL RESPIRATION. The passage of oxygen from an animal's environment into some distributing system of its body. *Cf.* INTERNAL RESPIRATION and RESPIRATION.

EXTRA-. Combining form, meaning "outside."

F_1 GENERATION. *See* FIRST FILIAL GENERATION.

F_2 GENERATION. *See* SECOND FILIAL GENERATION.

FACT. A real state of things as distinguished from a belief.

FACTORS. *See* GENES.

FALSE COELOM. *See* PSEUDOCOEL.

FAMILY. One of the subdivisions of an order; a group of next higher rank than a genus.

FATTY ACIDS. A group of organic acids formed by oxidation of alcohols.

FAUNA. The total of the animal life of a given region or period of time.

FEMALE GAMETE. *See* OVUM.

FERTILIZATION. The union of two gametes to form a single cell, the zygote. *Cf.* CONJUGATION.

- FIN.** An extension from the body of an aquatic animal which is used in locomotion.
- FIRST FILIAL GENERATION.** The individuals arising from a given mating. *Cf.* **SECOND FILIAL GENERATION.**
- FISSION.** The division of an organism into two or more parts; a method of reproduction.
- FLAGELLATE.** Having one or more flagella.
- FLAGELLUM** (*pl.* **FLAGELLA**). A long, hairlike extension from the free surface of a cell; capable of vibration and usually occurring singly. *Cf.* **CILIA.**
- FLUCTUATION.** A modification of a character that is conditioned by some change in the environment during development; a non-heritable variation. *Cf.* **MUTATION.**
- FOLLICLE.** A cellular sac or envelope.
- FOOD.** The material necessary for normal metabolism, that is, for protoplasmic maintenance and growth, the synthesis of secretions, and the transformation of energy in an organism.
- FOSSIL.** Anything of organic origin which was buried beneath the surface of the earth by natural causes in prehistoric times.
- FRATERNAL TWINS.** Two individuals, not necessarily of the same sex, that arise simultaneously from two zygotes in an animal that usually produces only one young at a time. *Cf.* **IDENTICAL TWINS.**
- FREE-LIVING.** Not sessile nor parasitic; capable of actively obtaining its own food.
- FUNCTION.** The action of any part of an organism. *Cf.* **STRUCTURE.**
- FUNGUS** (*pl.* **FUNGI**; *adj.* **FUNGOUS**). A colorless plant of relatively simple organization.
- GAMETE.** A differentiated germ cell. *Cf.* **TISSUE CELL.**
- GAMETOCYTE.** A cell capable of differentiating into a gamete.
- GAMETOGENESIS.** The differentiation of gametes. *Cf.* **HISTOGENESIS.**
- GANGLION.** A mass of nerve cell bodies.
- GASTRIC.** Pertaining to the stomach.
- GASTRULA.** A developing individual characterized by a diploblastic structure.
- GASTRULA CAVITY.** The cavity of the gastrula, lined with endoderm and opening by way of the blastopore; the archenteron.
- GASTRULATION.** The formation of a gastrula from a blastula by cell localization.
- GEL.** A semisolid or jelly-like state of protoplasm or any colloid. *Cf.* **SOL.**
- GENE-COMPLEX.** All the genes present in a zygote.
- GENERIC.** Pertaining to a genus.
- GENES.** The units of inheritance, transmitted from one generation to the next by way of the gametes and conditioning the appearance of an individual's characters during its development.
- GENE-STRING.** A linear series of genes constituting a linkage group; may be located in a chromonema.
- GENETICIST.** A student of heredity and variation; more specifically, a student of experimental breeding.
- GENETICS.** The science of heredity and variation.
- GENITAL.** Pertaining to the organs of reproduction.
- GENUS** (*pl.* **GENERA**). One of the subdivisions of a family; a group of next higher rank than a species.

- GERM CELL.** A cell, in a multicellular organism, that is capable of reproduction by syngamy. *Cf.* SOMATIC CELL and GAMETE.
- GERM LAYERS.** The cell layers resulting from the early cell localizations during the establishment of the body-plan in development; specifically, ectoderm, endoderm, and mesoderm. *Cf.* DIPLOBLASTIC and TRIPLOBLASTIC.
- GILL.** An organ of external respiration in aquatic animals.
- GILL SLIT.** One of the paired openings that appears in the region of the pharynx during the development of chordates and along the sides of which gills develop in the aquatic chordates.
- GLAND.** One or more cells differentiated for the production of some secretion.
- GONAD.** An organ in which gametes are differentiated; an ovary or testis.
- GONODUCT.** A duct through which gametes or embryos pass out of an animal.
- GONOPORE.** External opening of a reproductive duct.
- GROWTH.** The increase in volume of protoplasm that results when assimilation occurs at a more rapid rate than dissimilation.
- GROWTH PERIOD.** The period of gametogenesis that immediately precedes the meiotic divisions.
- GUSTATORY.** Pertaining to tasting.
- GUT.** The digestive tract.
- HABITAT.** The area or region in which an organism lives; the environmental conditions under which a species can exist.
- HAPLOID.** Having a single set of chromosomes which do not occur in pairs, as in gametes. *Cf.* DIPLOID.
- HEAD.** The front end of an animal, or part, if it is distinguished from the rest in any way.
- HEART.** A pulsating organ of the blood-vascular system; a blood vessel modified for propelling the blood.
- HEMOCÖEL.** A schizocöel or pseudocöel containing a fluid that can be called blood or lymph, and which is part of a circulatory system.
- HEMOGLOBIN.** The pigment of the blood with which oxygen combines to form oxyhemoglobin.
- HEPATIC.** Pertaining to the liver.
- HERBIVOROUS.** Feeding upon plants. *Cf.* CARNIVOROUS and OMNIVOROUS.
- HEREDITARY DETERMINERS.** *See* GENES.
- HEREDITARY UNITS.** *See* GENES.
- HEREDITY.** The resemblance of successive generations of individuals, conditioned by the transmission of genes during reproduction.
- HERITABLE VARIATION.** A modification in either structure or function which recurs in successive generations; a variation conditioned by changes in a gene or in a gene-complex. *Cf.* MUTATION, CHROMOSOMAL ABERRATION, and FLUCTUATION.
- HERMAPHRODITIC.** Possessing both male and female gonads.
- HETEROZYGOTE.** A zygote formed by the union of two gametes which differ with respect to particular genes. *Cf.* HOMOZYGOTE.
- HETEROZYGOUS.** Developing from a heterozygote. *Cf.* HOMOZYGOUS.
- HIBERNATION.** A cessation of activity by an animal during cold weather.
- HISTOGENESIS.** The differentiation of tissue cells. *Cf.* GAMETOGENESIS.
- HISTOLOGY.** The science of the structure of animals as revealed by the microscope; the study of cells as they are grouped to form tissues and organs. *Cf.* ANATOMY.

- HOMOLOGOUS CHROMOSOMES.** A pair of chromosomes similar in size and shape, one of which is contributed by each of the gametes that unite to form the zygote.
- HOMOLOGY** (*adj.* **HOMOLOGOUS**). Correspondence in fundamental structure. *Cf.* **ANALOGY**.
- HOMOZYGOTE.** A zygote formed by the union of two gametes which are alike with respect to particular genes. *Cf.* **HETEROZYGOTE**.
- HOMOZYGOUS.** Developing from a homozygote. *Cf.* **HETEROZYGOUS**.
- HORMONE.** *See* **ENDOCRINE**.
- HOST.** An organism that nourishes a parasite.
- HYBRID.** An individual whose parents differed with respect to one or more characters. *Cf.* **HYBRIDIZATION**.
- HYBRIDIZATION.** The breeding of individuals that differ with respect to one or more characters. *See* **EXPERIMENTAL BREEDING**.
- HYPER-.** Combining form, meaning "over," either in position or degree. *Cf.* **HYPOT-** and **SUPER-**.
- HYPOT-.** Combining form, meaning "under," either in position or degree. *Cf.* **HYPER-**.
- HYPOTHESIS.** A tentative correlation or explanation of observed facts which is usually stated as an aid to further study of related facts; if supported by additional data a hypothesis may become a theory.
- IDENTICAL TWINS.** Two individuals, always of the same sex, which arise during development from a single zygote. *Cf.* **FRATERNAL TWINS**.
- IMAGO.** Adult stage of an insect.
- IMPULSE.** *See* **NERVOUS IMPULSE**.
- INCURRENT.** Affording an entrance; leading inward. *Cf.* **EXCURRENT**.
- INDEPENDENT EFFECTOR.** A cell responding directly to changes in its environment; an effector that is independent of a reflex arc.
- INDIRECT CELL DIVISION.** *See* **MITOSIS**.
- INDIVIDUAL.** A physiologically balanced, living unit; an animal or plant.
- INGESTION.** The act of taking food into a place of digestion. *Cf.* **EGESTION**.
- INSTINCT.** Reflex action, frequently of a very complex character, dependent upon an inherited reflex arc.
- INTEGUMENT.** The outer covering of the body; the skin or a derivative of it.
- INTELLIGENCE.** The capacity to profit by experience, based upon analysis and association of ideas.
- INTER-.** Combining form, meaning "between" or "among."
- INTERNAL PARASITE.** *See* **ENDOPARASITE**.
- INTERNAL RESPIRATION.** The passage of oxygen from a distributing system, such as the blood vessels or the tracheæ, into the cells. *Cf.* **EXTERNAL RESPIRATION** and **RESPIRATION**.
- INTERNAL SECRETION.** *See* **ENDOCRINE**.
- INTRA-.** Combining form, meaning "within."
- INVAGINATION.** The movement of a group or layer of cells into a cavity. *Cf.* **EVAGINATION**.
- INVERTEBRATE.** An animal without a vertebral column or a notochord. *Cf.* **VERTEBRATE**.
- IRRITABILITY.** The capacity as a result of which protoplasm responds to stimuli; the capacity upon which coördination is dependent.
- ISOGAMETES.** Gametes of equal size that unite in pairs. *Cf.* **ANISOGAMETES**.

- ISOGAMY.** Fusion of gametes of equal size. *Cf.* ANISOGAMY and FERTILIZATION.
- ISOLECITHAL EGG.** An egg in which the yolk is not abundant and almost uniformly distributed throughout the cytosome. *Cf.* TELELECITHAL EGG.
- JUVENILE.** A self-sustaining young organism that is like the adult, except in size, after hatching, birth, or metamorphosis. *Cf.* EMBRYO and LARVA.
- LACUNA** (*pl.* LACUNÆ). A cavity or space.
- LAND BRIDGE.** A land connection between two other land regions; most often used for such a connection that has been submerged.
- LARVA** (*pl.* LARVÆ). A self-sustaining young organism that does not resemble the adult after hatching. *Cf.* EMBRYO and JUVENILE.
- LETHAL.** Capable of bringing about death.
- LEUCOCYTE.** A granular white blood cell; a non-pigmented or colorless blood cell. *Cf.* LYMPHOCYTE and ERYTHROCYTE.
- LIFE-CYCLE.** The history of an organism or species with reference to its methods of reproduction and development.
- LINEAR.** Like a line or thread.
- LINKAGE.** The occurrence of certain characters together in successive generations of individuals; a condition arising from the transmission of genes in linkage groups.
- LINKAGE GROUP.** A group of genes that is transmitted from one generation to the next as a unit. *Cf.* GENE-STRING.
- LOCUS** (*pl.* LOCI). A place; a locality.
- LOPHOPHORE.** A circlet of tentacles surrounding the mouth.
- LUMEN** (*pl.* LUMINA). A passageway or cavity.
- LUMINESCENCE.** The emission of light arising from chemical reactions within cells.
- LYMPH.** A circulating fluid consisting of plasma and white blood cells.
- LYMPH GLAND.** An organ in which lymphocytes are differentiated.
- LYMPHATIC.** A vessel which transports lymph.
- LYMPHOCYTE.** A non-granular white blood cell; a non-pigmented or colorless blood cell. *Cf.* LEUCOCYTE and ERYTHROCYTE.
- M.** Abbreviation for meter.
- MACRO-.** Combining form, meaning "large." *Cf.* MICRO-.
- MALE GAMETE.** *See* SPERMATOZOÖN.
- MALNUTRITION.** A condition resulting from any deficiency in nourishment.
- MAMMARY GLANDS.** Glands that secrete milk; characteristic of mammals.
- MANDIBULATE.** Possessing jaws, or mandibles, and thus able to bite.
- MATRIX** (*pl.* MATRICES). That which encloses anything; the intercellular material of sustentative tissues; the part of a chromosome surrounding the chromonemata.
- MATURATION.** The process of maturing or differentiation of the germ cells. *See* GAMETOGENESIS.
- MEIOSIS.** The process by which the number of chromosomes is changed from the diploid to the haploid number; brought about by two nuclear divisions following the growth period during gametogenesis. *Cf.* MITOSIS.
- MESENCHYME.** Loosely arranged cells of irregular shape which are relatively undifferentiated and give rise to different tissues.
- MESENTERY.** A double layer of cells connecting the visceral and parietal peritoneum and serving as a support for the coelomic organs.

- MESO-. Combining form, meaning "middle."
- MESODERM. The germ layer that is localized between the ectoderm and endoderm.
- MESODERMAL SOMITES. Compact, similar groups of mesodermal cells lying along each side of the neural tube.
- MESORCHIUM (*pl.* MESORCHIA). The mesentery supporting a testis.
- MESOVARIUM (*pl.* MESOVARIA). The mesentery supporting an ovary.
- META-. Combining form, meaning "behind" in position or "later" in time.
- METABOLIC CELL. A cell that is not in the process of division; sometimes called a resting cell.
- METABOLISM. The capacity as a result of which protoplasm is synthesized and destroyed in such a way that the organism lives. *Cf.* ASSIMILATION and DIS-SIMILATION.
- METAGENESIS. A type of life-cycle in which a sexually reproducing organism arises from and gives rise to an asexually reproducing organism.
- METAMERE. *See* SOMITE.
- METAMERISM. The condition of being divided into a number of similar parts, arranged in linear series and called metameres or somites.
- METAMORPHOSIS. The alteration of structure which an animal undergoes after it hatches; specifically, the transformation of a larva into an adult.
- METAZOA (*sing.* METAZOÖN or METAZOAN). Multicellular animals. *Cf.* PROTOZOA.
- METER. A measure of length equal to 39.37 inches.
- MICRO-. Combining form, meaning "small." *Cf.* MACRO-.
- MIGRATION. A movement of animals into a new locality, usually in search of food.
- MILLIMETER. The thousandth part of a meter; the tenth part of a centimeter; one inch equals 25.4 millimeters.
- MISSING LINK. *See* SYNTHETIC TYPE.
- MITOSIS. The process of indirect nuclear division during which chromosomes appear and are split longitudinally, the halves of each one passing into separate nuclei; cells arising after mitosis contain the diploid number of chromosomes. *Cf.* AMITOSIS and MEIOSIS.
- MM. Abbreviation for millimeter.
- MOLT. To shed an exoskeleton or any integumentary structure.
- MONOBLASTIC. Having a closed cavity surrounded by a single layer of cells. *Cf.* DIPLOBLASTIC and TRIPLOBLASTIC.
- MONECIOUS. Without sexually differentiated individuals; having male and female gonads in the same individual. *Cf.* DIOECIOUS and HERMAPHRODITIC.
- MORPHOLOGY. The science of structure.
- MOUTH. The opening of the digestive tract through which ingestion occurs.
- MOUTH CAVITY. The part of the digestive tract into which food is first taken.
- MOUTHPARTS. The appendages related to the mouth of an arthropod.
- MUCOSA. The cellular lining of the digestive tract, derived from endoderm.
- MUCUS (*adj.* MUCOUS). A sticky fluid secreted by certain glands.
- MULTI-. Combining form, meaning "many." *Cf.* UNI-.
- MUTATION. A modification of a character that is conditioned by some change in the gene-complex; a heritable variation; specifically, an alteration of a gene. *Cf.* FLUCTUATION.
- NASAL. Pertaining to the nose or nostril.
- NEPHRIDIUM (*pl.* NEPHRIDIA). An excretory tubule found in arthropods, mollusks, and some other animals.

- NERVE. A bundle of nerve fibers lying outside the central nervous system.
- NERVE CELL. *See* NEURON.
- NERVE CORD. A compact cord composed of neurons and forming part of a central nervous system; it may or may not be ganglionated. *Cf.* CONNECTIVE.
- NERVE FIBERS. Extensions of the cytosome of a neuron; dendrites and axons.
- NERVE NET. The association of neurons to form a net in which the nerve fibers are continuous.
- NERVE RING. A circular nerve cord.
- NERVOUS COÖRDINATION. Coördination brought about by the reaction of parts to the discharge of nervous impulses. *Cf.* COÖRDINATION and CHEMICAL COÖRDINATION.
- NERVOUS IMPULSE. Something established and transmitted in a neuron as a result of a stimulus.
- NEURAL. Pertaining to the nervous system.
- NEUROID. Pertaining to nervous structure or function, but not identical with term "neural." *Cf.* NEUROID TRANSMISSION.
- NEUROID TRANSMISSION. Transmission of a stimulus from cell to cell and in all directions; in contrast to transmission through nerve cells.
- NEURON. A nerve cell; a cell characterized by conspicuous extensions of the cytosome, known as dendrites and axons, over which nervous impulses pass.
- NOCTURNAL. Pertaining to the night. *Cf.* DIURNAL.
- NOTOCHORD. A cellular cord formed between the archenteron and the neural tube during the early development of all chordates; the vertebral column is formed around but not from the notochord in vertebrates.
- NUCLEUS (*pl.* NUCLEI). The part of the cell containing the chromatin and limited by the nuclear membrane.
- NUTRITION. The science of foods; the basic processes or manner of obtaining foods.
- NYMPH. The stage in development of an insect between the larva and the adult; the pupa or chrysalis stage.
- OLFACTORY. Pertaining to the sense of olfaction, or smell.
- OMNIVOROUS. Feeding upon both plants and animals. *Cf.* CARNIVOROUS and HERBIVOROUS.
- ONTOGENETIC. Related to the origin and development of the individual. *Cf.* PHYLOGENETIC.
- OÖGENESIS. The differentiation of the ova. *Cf.* SPERMATOGENESIS.
- OPHTHALMIC. Pertaining to the eye.
- OPTIC. Pertaining to vision or to the eye.
- ORAL. Pertaining to the mouth, or place of ingestion.
- ORDER. One of the subdivisions of a class; a group of next higher rank than a family.
- ORGAN. A group of tissues associated together for the performance of a special function. *Cf.* SYSTEM.
- ORGANIC. Pertaining to or resulting from the activities of organisms.
- ORGANIC EVOLUTION. The process of descent with modification as a result of which present-day species of animals have arisen from those of the past. *Cf.* EVOLUTION.
- ORGANISM. An animal or plant.
- ORGAN-SYSTEM. *See* SYSTEM.

OSTIUM. An opening or entrance.

OVARY. A gonad in which ova undergo differentiation. *Cf.* TESTIS.

OVIPAROUS. Egg-laying; producing young which develop from eggs that hatch outside the body of the mother. *Cf.* OVOVIVIPAROUS and VIVIPAROUS.

OVOVIVIPAROUS. Producing young which develop from eggs that hatch within the body of the mother. *Cf.* OVIPAROUS and VIVIPAROUS.

OVULATION. The discharge of eggs from the ovary.

OVUM (*pl.* OVA). A mature or differentiated female germ cell; a macrogamete. *Cf.* SPERMATOZOÖN.

PALEONTOLOGY. The science of the distribution of animals over the surface of the earth at successive periods of time. *Cf.* ZOÖGEOGRAPHY.

PALP. A feeler.

PAPILLA (*pl.* PAPILLÆ). A rounded, thick process or extension.

PARASITE. An organism that lives in or on another, at the expense of the latter. *Cf.* HOST.

PARASITISM. An association of organisms of two species in which only one, the parasite, is benefited. *Cf.* COMMENSALISM and SYMBIOSIS.

PARIETAL. Pertaining to walls; specifically, to the lining of the cœlom.

PARTHENOGENESIS. The development of an egg without union with a spermatozoön; may be natural or follow an artificial activation.

PEDAL. Pertaining to the foot.

PEDOGENESIS. Reproduction by individuals that are not adult.

PELAGIC. Living at or near the surface of the ocean at some distance from land.

PELLICLE. A delicate layer surrounding a cell, as in some Protozoa.

PENIS (*pl.* PENES). An organ functioning during sexual union and characteristic of the males of many species.

PERI-. Combining form, meaning "around" or "near."

PERICARDIAL. Surrounding the heart.

PERICARDIUM. The peritoneum of the pericardial cavity; also used for the pericardial cavity and its walls.

PERIPHERAL. Related to or situated on or toward the surface.

PERISTOME. Membranous area surrounding the mouth.

PERITONEUM. The compact cellular layer of mesodermal origin that lines the cœlom of many animals.

PHENOMENON (*pl.* PHENOMENA). A directly observed fact.

PHOBOTAXIS (*pl.* PHOBOTAXES). Response of a lower organism to light, chemicals, etc. *Cf.* TROPISM.

PHYLOGENETIC. Related to the origin and evolution of a species or other group of organisms. *Cf.* ONTOGENETIC.

PHYLUM (*pl.* PHYLA). One of the major subdivisions of the Animal and Plant Kingdoms.

PHYSIOLOGICAL BALANCE. Functional unity of a cell or organism, resulting either from lack of cell specialization or from well-developed coördination.

PHYSIOLOGY. The science of function.

PIGMENT. Organic coloring matter.

PLACENTA (*pl.* PLACENTÆ). The organ by means of which the mammalian embryo is nourished during development; derived in part from the uterine wall and in part from embryonic membranes.

PLASMA. The liquid portion of the blood and lymph.

- PLEURAL.** Pertaining to the cavity surrounding the lungs or to the membrane lining such a cavity.
- POLAR AXIS.** An axis between two opposite poles. *Cf.* POLARITY.
- POLAR BODY.** A small, non-functional cell produced at each meiotic division in oögenesis; there will be three of these if the first polar body divides at the time of the second meiotic division.
- POLARITY.** Existence in different parts of an organism, or of a non-living body, of opposite properties. *Cf.* POLAR AXIS.
- POLLINATE.** To convey pollen, produced by male organs, to the female organs in plants.
- POLOCYTES.** The polar bodies.
- POLY-.** Combining form, meaning "many."
- POLYEMBRYONY.** The development of several embryos from one zygote.
- POLYP.** Any animal with many footlike processes; specifically, one of the individuals of a coelenterate colony.
- POPULATION.** A group of individuals of the same species that do not have the same genetic constitution and consequently give rise to new combinations in successive generations; pure lines can be sorted out of a population by selection. *Cf.* PURE LINE.
- POSTERIOR.** Pertaining to or situated near the end away from the head; the hind part of an animal or part; opposite to anterior.
- PREDATORY.** Capturing other animals for food.
- PREHENSILE.** Fitted for grasping or holding.
- PREHUMAN.** Existing before the appearance of man upon the earth.
- PRIMATE.** A member of the Order Primates, which includes all kinds of monkeys, the lemurs, and man.
- PRIMORDIAL.** First in order; primitive.
- PRIMORDIUM** (*pl.* PRIMORDIA). A beginning.
- PROCTODEUM** (*pl.* PROCTODEA). The ectodermal invagination which forms the most posterior part of the digestive tract during development. *Cf.* STOMODEUM.
- PRONUCLEUS** (*pl.* PRONUCLEI). The nucleus of a gamete; contains the haploid number of chromosomes.
- PROPAGATION.** The increase in numbers resulting from reproduction.
- PROTOPLASM.** The complex colloidal material of which all organisms are composed; the physico-chemical basis of life.
- PROTOZOA** (*sing.* PROTOZOON or PROTOZOAN). The phylum of the unicellular animals; unicellular animals. *Cf.* METAZOA.
- PROTOZOÖLOGY.** The science of Protozoa.
- PROTRACTOR MUSCLE.** A muscle that extends a part or draws it forward. *Cf.* RETRACTOR MUSCLE.
- PROXIMAL.** Situated toward the center or place of attachment. *Cf.* DISTAL.
- PSEUDOCÆL.** A cavity within the mesoderm that is well organized but lacks the features typical of a coelom; a "false coelom." *Cf.* BODY CAVITY, SCHIZOCÆL, and HEMOCÆL.
- PSEUDOCÆL.** A body cavity in some invertebrates superficially resembling a coelom but not surrounded by mesoderm.
- PSEUDOPodium** (*pl.* PSEUDOPODIA). A temporary protrusion of a cell by means of which locomotion is effected.
- PULMONARY.** Pertaining to the lungs.

PULMONATE. Having lungs or lunglike structures as organs of external respiration.
Cf. BRANCHIATE.

PURE LINE. A group of individuals of the same species that are homozygous for some particular character or characters and consequently breed true; variations in a pure line are usually fluctuations. *Cf.* POPULATION.

PYLORIC. Pertaining to the opening between the stomach and intestine.

RADIAL SYMMETRY. Symmetry in all planes passing through a longitudinal axis, as in a cylinder, or in which parts are arranged around an axis like the spokes of a wheel.

REASSOCIATION. The coming together of parts that previously have been artificially separated.

RECEPTION. The process which occurs in a receptor; the initial response to a stimulus.

RECEPTOR. A region which is especially sensitive to changes in the environment; may be a sensory cell or a complex sense organ.

RECESSIVE GENE. A gene that is without appreciable effect when associated with its dominant allelomorph. *Cf.* DOMINANCE.

RED BLOOD CELL. *See* ERYTHROCYTE.

REFLEX ACTION. An automatic response to a stimulus; the functional basis of nervous coördination.

REFLEX ARC. An afferent and efferent neuron, with or without adjustor neurons, so associated as to conduct a nervous impulse from a receptor to an effector; the structural basis of nervous coördination.

REGENERATION. The process of replacing a lost part.

RENAL. Pertaining to the kidney.

REPRODUCTION. The capacity as a result of which certain parts can become detached and, either alone or after union with protoplasm of another organism of the same kind, give rise to a new individual capable of becoming like the parent or parents in all essential respects; the capacity upon which continuity of a species depends.

REPRODUCTIVE ORGAN. *See* GONAD.

RESEARCH. Continued search after facts and principles.

RESPIRATION. The delivery of oxygen to the protoplasm of all cells, either directly by diffusion from a surrounding fluid, as in the Protozoa and simple Metazoa, or indirectly by means of respiratory organs and distributing systems. *See* EXTERNAL RESPIRATION and INTERNAL RESPIRATION.

RESPIRATORY. Pertaining to respiration.

RETRACTOR MUSCLE. A muscle that withdraws a part or pulls it backward. *Cf.* PROTRACTOR MUSCLE.

RUDIMENTARY. Embryonic; not completely developed; having no function; frequently but not correctly used to mean vestigial.

SCHEMATIC. Made or done according to a fundamental plan.

SCHIZOCOEL. A small cleft-like cavity within the mesoderm, an intercellular space; pseudocoels arise by enlargement or by union of schizocoels.

SCIENCE. Knowledge gained by systematic observation, experimentation, and reasoning; factual information, correlated and systematized.

SECOND FILIAL GENERATION. The individuals produced by mating parents from a given F_1 generation. *Cf.* FIRST FILIAL GENERATION.

- SECRETION.** The synthesis of a substance necessary for normal function in the organism; the passage of such substance from the cell; the substance itself.
- SEDENTARY.** Remaining in one place; not free-swimming, as a tube-dwelling animal. *Cf.* **SESSILE.**
- SEGMENT.** A part cut off or marked as separate from others; a natural division of the body or a part of it. *Cf.* **SOMITE.**
- SEGREGATION.** The separation of allelomorphic genes and their distribution into separate cells during one of the meiotic divisions. *Cf.* **DISJUNCTION.**
- SELF-FERTILIZATION.** Union of gametes produced by the same individual which may occur in some hermaphroditic organisms. *Cf.* **CROSS-FERTILIZATION.**
- SEMINAL.** Pertaining to or containing spermatozoa.
- SEMINIFEROUS TUBES.** Tubes of the testis along the walls of which the spermatozoa are differentiated.
- SENSE ORGAN.** A multicellular receptor; an organ containing a part which is especially sensitive to some particular type of stimulus.
- SENSORY CELL.** A unicellular receptor.
- SEPTUM** (*pl.* **SEPTA**). A partition between two cavities.
- SERUM.** The liquid that separates from a blood clot; blood serum contains no cells or fibrin.
- SESSILE.** Attached; not free-swimming. *Cf.* **SEDENTARY.**
- SETA** (*pl.* **SETÆ**). A bristle.
- SEX.** A characteristic condition of animals in which the individuals are either male or female and are distinguished essentially by the production of spermatozoa or ova, respectively.
- SEX CHROMOSOMES.** Chromosomes that differ in number and distribution in the males and females of a species; the X- and Y-chromosomes. *Cf.* **AUTOSOMES.**
- SEX-LINKED INHERITANCE.** The inheritance of characters conditioned by genes carried by the X-chromosomes.
- SEX-REVERSAL.** The loss of original sex characters and the assumption of those of the opposite sex.
- SEXUAL REPRODUCTION.** Reproduction by union of gametes like those produced by sexually differentiated individuals; since anisogametes are almost universally differentiated, this term is commonly used as a synonym for reproduction by syngamy. *Cf.* **ASEXUAL REPRODUCTION.**
- SEXUAL UNION.** Temporary association of male and female organisms during which sperm are introduced into the reproductive tract of the female.
- SILICEOUS.** Containing or consisting of silica or quartz, which is characteristic of sand.
- SINUS** (*pl.* **SINUS** or **SINUSES**). A cavity.
- SIPHON.** A canal.
- SKELETON.** The hard parts of an organism which serve to support and protect soft parts. *Cf.* **ENDOSKELETON** and **EXOSKELETON.**
- SOCIAL.** Living in groups. *Cf.* **SOLITARY.**
- SOL.** A liquid state of protoplasm or any colloid. *Cf.* **GEL.**
- SOLITARY.** Living alone. *Cf.* **SOCIAL.**
- SOMATIC.** Pertaining to the body of an organism.
- SOMATIC CELL.** A cell, in a multicellular organism, that has lost the capacity for reproduction. *Cf.* **GERM CELL** and **TISSUE CELL.**
- SOMITE.** One of a series of homologous parts arranged in a row. *Cf.* **SEGMENT.**
- SPECIES** (*pl.* **SPECIES**). A subdivision of a genus, sometimes separated into varieties.

SPERM. *See* SPERMATOZOÖN.

SPERMATOGENESIS. The differentiation of the spermatozoa. *Cf.* OÖGENESIS.

SPERMATOZOÖN (*pl.* SPERMATOZOA). A mature or differentiated male germ cell; a microgamete. *Cf.* OVUM.

SPERMIOGENESIS. The cytosomal differentiation of a spermatozoön; the transformation of a spermatid into a spermatozoön.

SPINAL. Pertaining to the vertebral column.

SPORULATION. Reproduction by multiple fission.

STERNAL. Pertaining to the ventral mid-region of arthropods; pertaining to the breastbone, or sternum, of vertebrates.

STIMULUS (*pl.* STIMULI). A change in the environment.

STOMODEUM (*pl.* STOMODEA). The ectodermal invagination which forms the mouth cavity during development. *Cf.* PROCTODEUM.

STROBILIZATION. A method of reproduction by linear budding.

STRUCTURE. The arrangement or organization of parts of an organism. *Cf.* FUNCTION.

SUB-. Combining form, meaning "under" or "below."

SUBSTRATUM (*pl.* SUBSTRATA). Anything which underlies or supports; a substrate.

SUPER-. Combining form, meaning "over"; same as HYPER-; opposite to SUB-.

SUPERFICIAL. Lying on or near the surface.

SUPRA-. Combining form, meaning "above"; same as SUPER-.

SYMBIOSIS. An association of organisms of two species in which both are benefited. *Cf.* PARASITISM and COMMENSALISM.

SYMMETRY. The reversed repetition of parts around an axis or on opposite sides of any plane, so that mirrored halves result from a separation along the axis or plane of symmetry.

SYNAPSE. The place of contact between two nerve fibers.

SYNOPSIS. The temporary pairing of homologous chromosomes which precedes the first meiotic division; occurs during the growth period.

SYNGAMY. *See* FERTILIZATION.

SYNTHESIS. The building-up of a chemical compound from simpler compounds or molecules.

SYNTHETIC TYPE. A species that represents an intermediate condition between well-recognized groups of organisms; a primitive ancestral type from which more highly specialized types have arisen.

SYSTEM. A group of structurally related organs performing some general function.

TACTILE. Pertaining to the sense of touch.

TAXIS. *See* TROPISM and PHOBOTAXIS.

TAXONOMY. The science of classification.

TELEOCITHAL EGG. An egg in which the yolk is abundant and concentrated in and toward the vegetal hemisphere. *Cf.* ISOLECITHAL EGG.

TENTACLE. An elongated, flexible, cellular process of the body.

TERRESTRIAL. Living on the ground.

TESTIS (*pl.* TESTES). A gonad in which spermatozoa undergo differentiation. *Cf.* OVARY.

THEORY. A conception of how something has been brought about; an explanation or correlation of observed facts; theories may be disproved, because they are the products of man's thinking.

THERMAL. Pertaining to heat.

THORAX (*pl.* THORACES). A part of the body between the head and abdomen.

TISSUE. A group of somatic cells differentiated in the same way for the performance of the same function.

TISSUE CELL. A differentiated somatic cell. *Cf.* GAMETE.

TOTIPOTENT CELL. An undifferentiated cell.

TRACHEA (*pl.* TRACHEÆ). An air-tube; specifically, the air-passage from the larynx to the bronchi in vertebrates.

TRANSFORMATION OF ENERGY. The process of changing potential energy (energy of configuration or position) into kinetic energy (energy of motion), or the reverse process; in protoplasm, potential energy is stored in the complex chemical molecules and released, or transformed, by the disintegration of these into simpler molecules; the transformation of potential into kinetic energy is always accompanied by the production of heat; the activities of organisms are dependent upon the release of kinetic energy.

TRANSMISSION. The passage of a nervous impulse through a neuron.

TRIPLOBLASTIC. Having three cell layers, ectoderm, endoderm, and mesoderm, a digestive cavity lined with endoderm, and usually a coelom. *Cf.* MONOBLASTIC and DIPLOBLASTIC.

TROPISM. Preferably defined as a forced reaction given to certain stimuli by sessile animals and plants, although often used as a synonym of PHOBOTAXIS and TAXIS.

TRUE COELOM. *See* COELOM.

TYPHLOSOLE. A single thick invagination of the wall of the digestive tract in some invertebrates. *Cf.* VILLUS.

ULTRAMICROSCOPIC. Too small to be seen with a microscope.

UMBILICAL CORD. A cord containing blood vessels and extending from an embryo to its placenta.

UMBO (*pl.* UMBONES). A domelike projection of each valve near the hinges of the shells of certain mollusks.

UNI-. Combining form, meaning "one." *Cf.* MULTI-

UNIVERSAL SYMMETRY. Symmetry in any plane passing through a diameter of a spherical mass.

URINARY. Pertaining to urine.

URINO-GENITAL. Pertaining to the excretory and genital organs.

UTERUS (*pl.* UTERI). An expanded portion of an oviduct in which zygotes develop.

VALVE. Any part of an organism that resembles a hinged door; specifically, thin folds that control the direction of flow of blood and lymph, and the parts of the shell of pelecypods and brachiopods.

VARIATION. The lack of resemblance between the individuals of a species; may or may not be heritable.

VARIETY. A subdivision of a species.

VAS (*pl.* VASA). *See* VESSEL.

VASCULAR. Pertaining to the circulation of fluids.

VEGETAL HEMISPHERE. That half of a telolecithal egg which does not contain the nucleus and is filled with yolk. *Cf.* ANIMAL HEMISPHERE.

VEGETAL POLE. A point on the surface of an egg opposite the animal pole; one end of the egg-axis.

VEGETATIVE CELL. *See* METABOLIC CELL.

- VEIN. A blood vessel carrying blood from capillaries toward the heart. *Cf.* ARTERY.
- VENTRAL. Pertaining to or situated near the surface away from the back; the lower part of an animal or part; opposite to dorsal.
- VENTRICLE. A hollow part or organ; a cavity; specifically, the ventricle of many hearts and the ventricles of the vertebrate brain.
- VERMES. *See* WORM.
- VERTEBRA (*pl.* VERTEBRÆ). One of the ringlike segments composing the vertebral column, or backbone.
- VERTEBRATE. An animal possessing a vertebral column. *Cf.* INVERTEBRATE.
- VESICLE. Any small, saclike structure.
- VESSEL. A tube, or canal, by which a fluid is conducted; usually restricted to those carrying blood and lymph. *Cf.* DUCT.
- VESTIGIAL. Any organ at a given stage of development that is less developed in one individual than in another is vestigial in the former; having been better developed at an earlier stage of development or in a lower organism. *Cf.* RUDIMENTARY.
- VILLUS (*pl.* VILLI). A minute, fingerlike projection, containing blood vessels and occurring in great numbers, as in the intestine of vertebrates. *Cf.* TYPHLOSOLE.
- VISCERA (*sing.* VISCUS). The internal organs of the body; specifically, the organs surrounded by the coelom.
- VISUAL. Pertaining to sight.
- VITAMINS. A group of organic compounds, occurring in small quantities in certain foods, which are necessary for normal metabolism.
- VIVIPAROUS. Giving birth to young that develop from eggs within the body of the mother and are nourished from the blood stream of the mother. *Cf.* OVIPAROUS and OVOVIVIPAROUS.
- WHITE BLOOD CELL. *See* LEUCOCYTE and LYMPHOCYTE.
- WORM. In popular language, any small creeping animal; specifically, such animals are found in many different groups, as, for example, the Platyhelminthes, Nematoda, and Annelida.
- X-CHROMOSOME. A sex chromosome that is paired in one sex and single in the other, where it may or may not be associated with a Y-chromosome.
- Y-CHROMOSOME. A sex chromosome that occurs in only one sex, if at all, and is not paired; carries very few genes.
- YOLK. Complex food material stored in a female germ cell or an associated cell and used during development.
- ZOÖGEOGRAPHY. The science of the distribution of animals over the surface of the earth at a given period of time. *Cf.* PALEONTOLOGY.
- ZOÏD. Any member of an animal colony; specifically, one of the individuals of a bryozoan colony.
- ZOÖLOGY. The science of animal life.
- ZYGOTE. A cell produced by the union of two gametes.

INDEX

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